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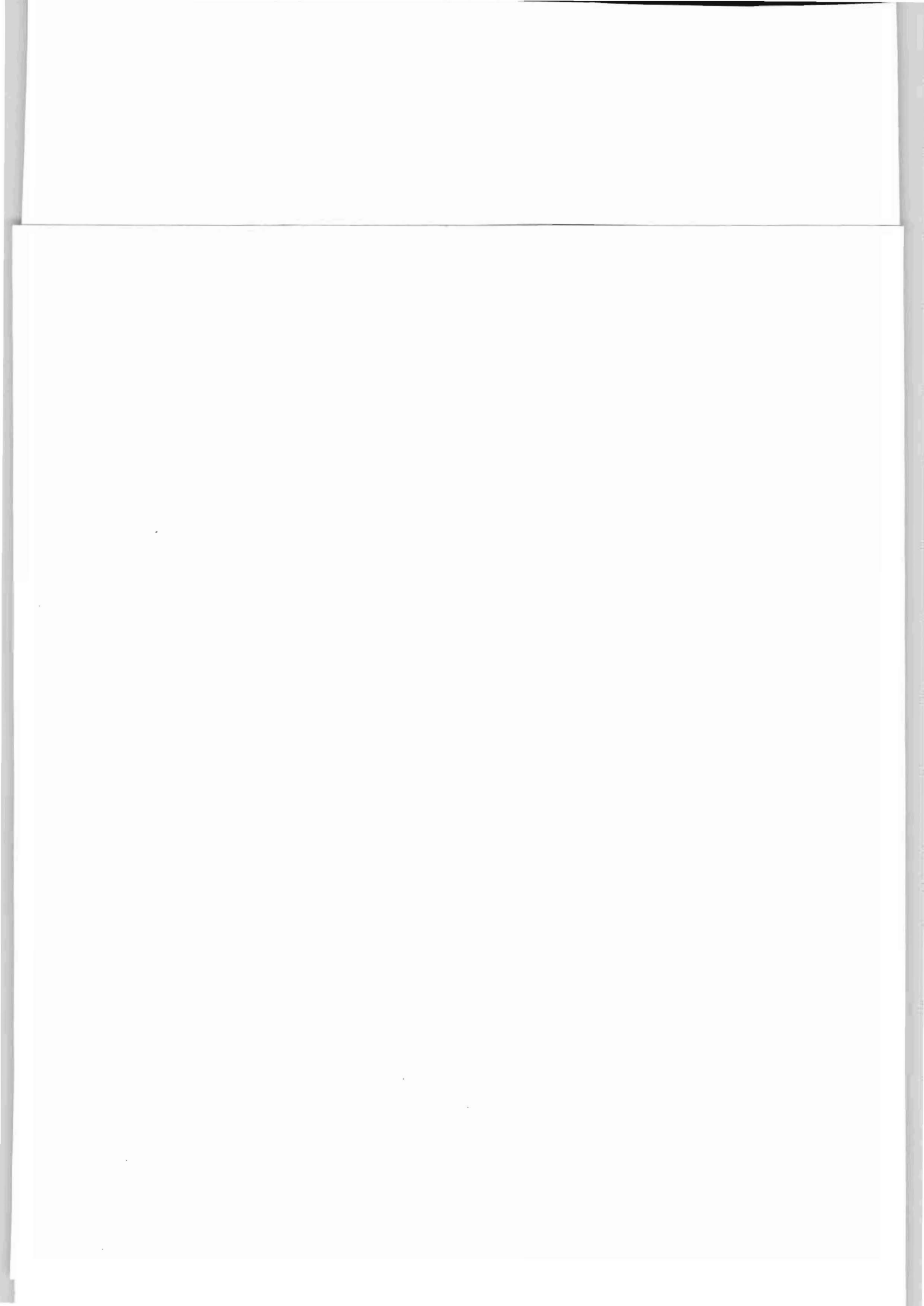


Signe H. Skjæveland

ECOLOGY OF ECHINODERMS IN BORGENTJORDEN,

NORTH-TRØNDELAG, NORWAY

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ABSTRACT

This one-year investigation in Borgenfjorden, an estuary with two basins in the inner part of Trondheimsfjorden, was carried out by monthly diving along seven transect lines around the fjord. Large differences both in the biomass values, number of species and specimens were found between the two basins. This is supposed to be due to anaerobic bottom conditions in the inner basin.

Only the three most common of the 22 echinoderm species found have been treated here, namely Asterias rubens, Ophiura texturata and Ophiura albida. A. rubens made up 84% of the total echinoderm biomass estimated at $(6.1 \pm 1.3) \text{ g/m}^2$ dry weight. The time of spawning for the three species is determined, and an examination of stomach content of the two ophiuroid species has been carried out.

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INTRODUCTION

Nearly half a century has gone by since the first scientific investigation was carried out in Borgenfjorden (Nordgaard 1923). In his work Nordgaard lists the benthic animals found and the algae, fishes and mammals. In the autumn of 1967, another investigation in this area was initiated (Borgenfjordundersökelsene 1969), intending to give a qualitative and quantitative description of the main benthic faunal elements.

I was given the opportunity to work on the echinoderms from the autumn 1969 for my Cand. real. thesis. This paper is prepared from the thesis, delivered at the University of Trondheim in spring 1972 (Skjæveland 1972). The three dominant species, Asterias rubens, Ophiura texturata, and Ophiura albida are more thoroughly treated. The main purpose was to estimate biomass values of the echinoderms throughout a year, and to study aspects of the biology of the three species.

AREA AND ENVIRONMENT

Topography

Borgenfjorden is a landlocked fjord in the inner part of Trondheimsfjorden (Fig. 1). The surface area is estimated at 19.3 km^2 at high water line, and 17.1 km^2 at low water line. The narrow inlet at Strømmen (Fig. 2) has a width of about 150 m and a depth of 5-8 m. The fjord itself is divided into two basins by a threshold at Bosnes (Fig. 2), where the width is about 1 km and the depth 14 m. The maximum depth is 40 m in the outer basin and 30 m in the inner basin.

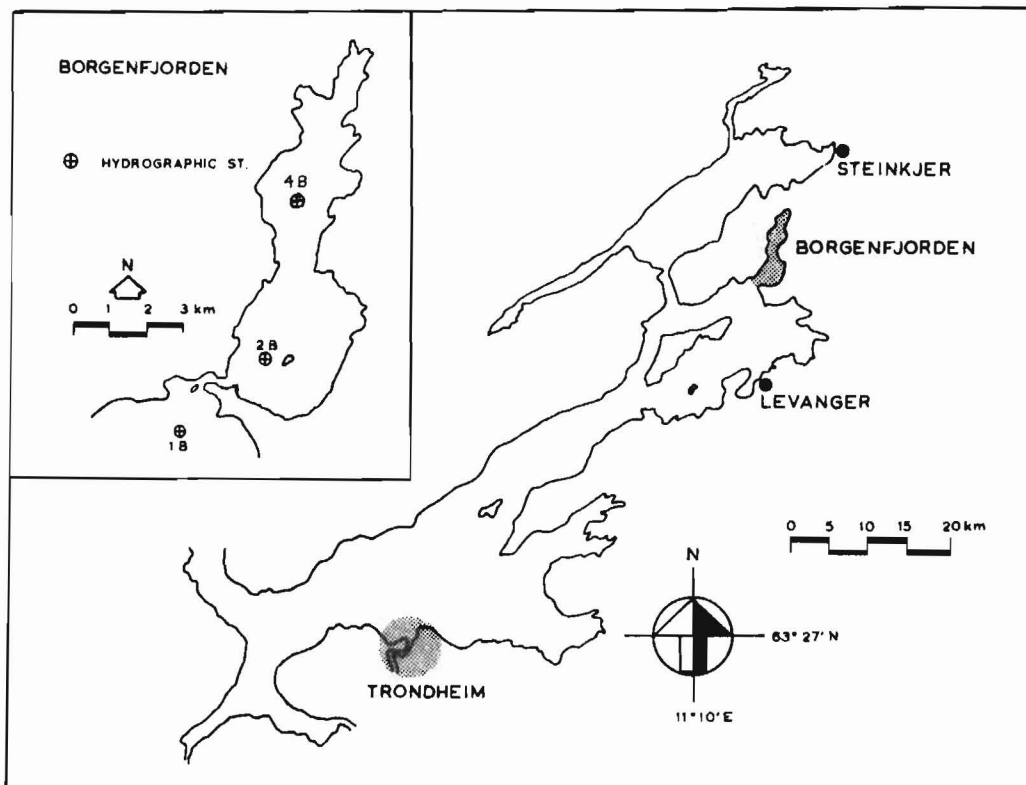


Fig. 1. Map of Trondheimsfjorden and positions of the hydrographic stations in Borgenfjorden.

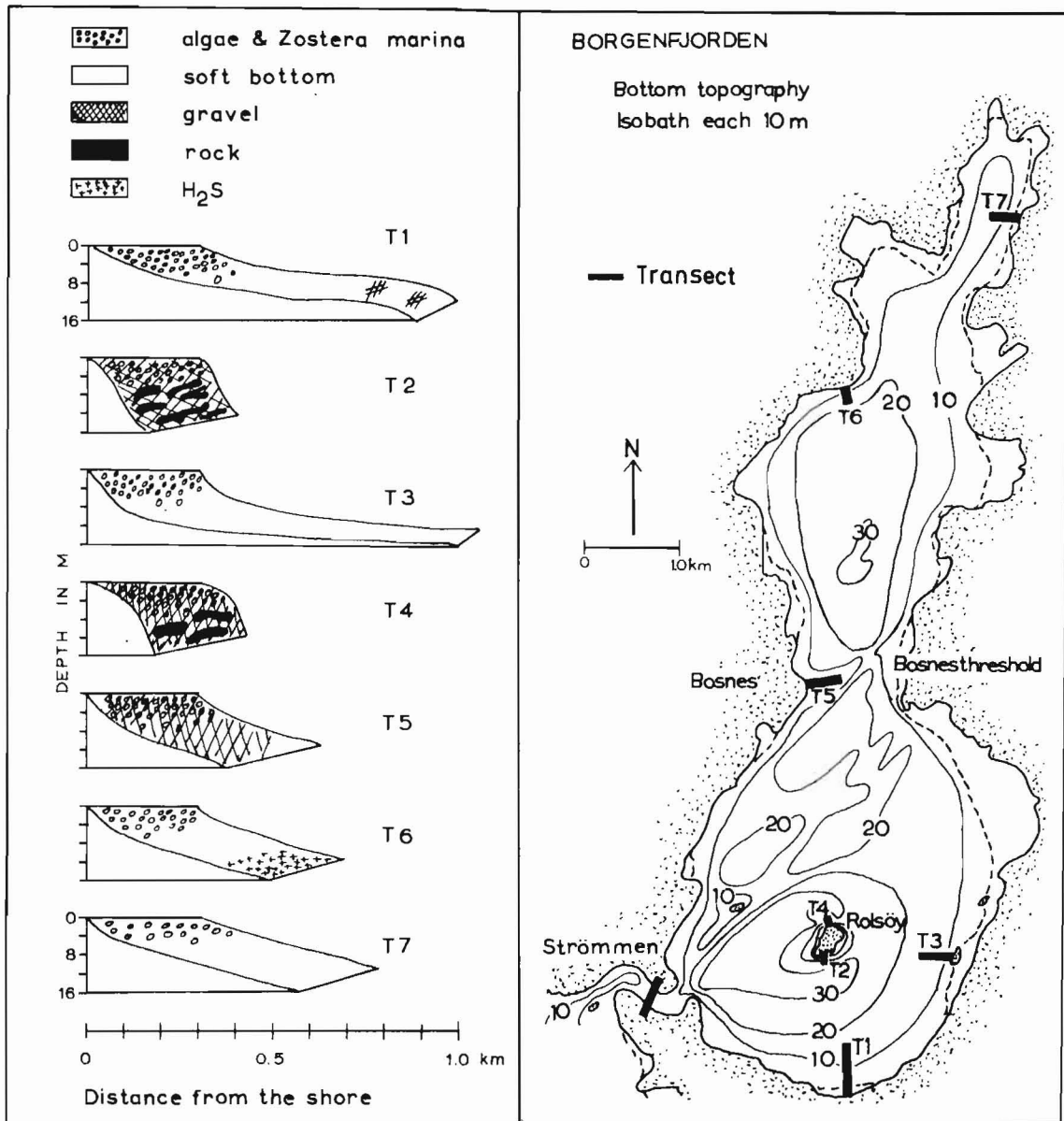


Fig. 2. Map of Borgenfjorden with line transects, bottom topography and the localities mentioned in the text. Longitudinal sections and bottom descriptions of the line transects (T1-T7). (Partly after Gulliksen 1973).

Sedimentology and hydrography

These subjects have been described by Gulliksen (1972) and McClimans (in press), and only a brief account will be presented here. The distribution of the bottom sediments in Borgenfjorden are shown in Fig. 3. Bare rock is found around Rolsøy, and hard bottom with gravel and sand is found in areas exposed to current. The greater parts of the bottom are covered with clay. The soft bottom material has a high content of organic matter (Strömngren et al. 1971).

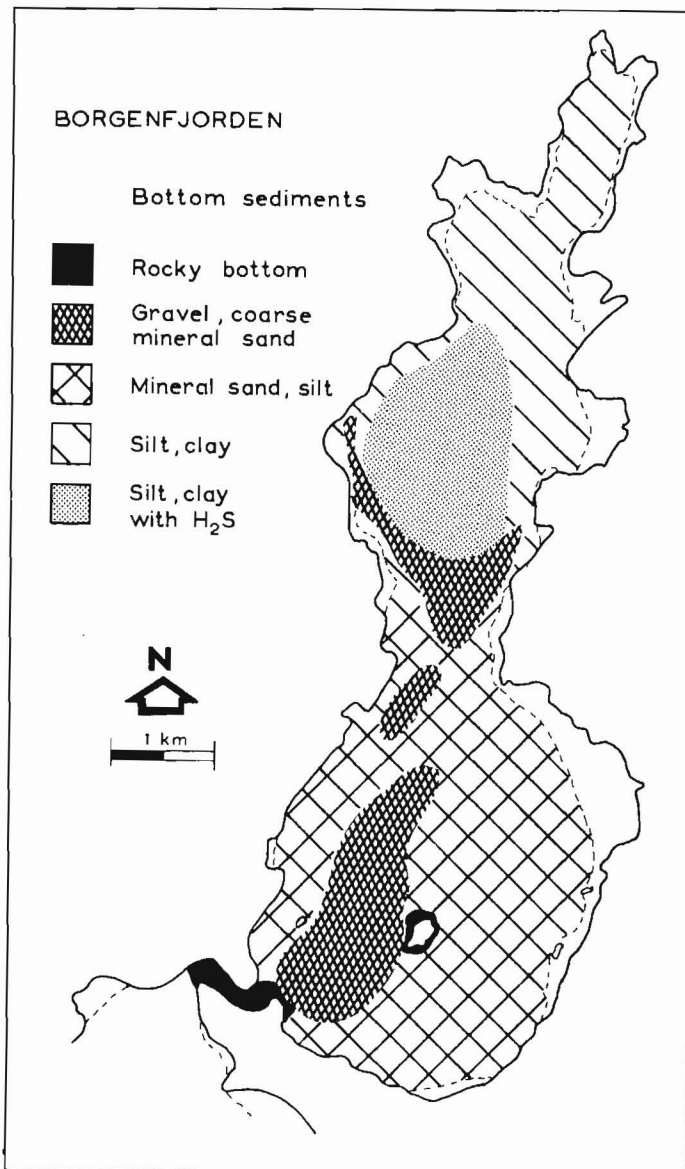


Fig. 3. Bottom sediments of Borgenfjorden (after Gulliksen 1971)

The tidal current through the narrow entrance at Strømmen causes a strong turbulence in the outer basin, and the stability of the water masses at St. 2B (Fig. 1) is very low in all seasons, and the oxygen content is high. By passing the Bosnes threshold to the inner basin, however, the tidal current loses much energy and the turbulence influences mainly the upper 10-15 m. A thermocline is formed during the summer so that cold water is trapped below threshold level. The oxygen content at the bottom is low and H_2S is observed towards late summer. The stability reduces as the temperature falls, and in late autumn the bottom water is renewed.

The temperature ranges from 1 to $16^{\circ}C$, and the salinity was never below $24^{\circ}/\text{oo}$ during the investigation period.

Description of the transects

The sampling was done on a transect line from the shore and down to 16 m depth on seven stations (Fig. 2) which were selected to give a best possible coverage of the variations in substrate, hydrography and distance from the mouth of the fjord.

A survey of the benthos algae in Borgenfjorden is given by Evensen (1971), and a detailed description of each transect according to substrate and vegetation is given by Gulliksen (1973). Therefore only a summary is given here:

Transects 1 and 3 have mainly soft bottom with some gravel. Transect 5 has mixed bottom with clay, gravel and rocks. Transects 2 and 4 have mainly hard bottom, and these are the two transects most exposed to current. On all five of these transects in the outer basin, benthos algae grow in the upper 8 m. Transects 6 and 7 in the inner basin have very soft bottom and sparse vegetation, especially on transect 7. At 16 m depth on transect 6, H_2S is registered in the sediments during the summer.

MATERIAL AND METHODS

The material was collected by diving, sampling with a Petersen 0.1 m² grab, trawling, and dredging in Borgenfjorden and just outside Strømmen (Fig. 2). Diving was done from July 1969 to September 1970. Sampling with the Petersen 0.1 m² grab was initiated in September 1967 (Borgenfjordundersøkelsene 1969), and the material found has been examined until October 1970. Trawling and dredging were carried out occasionally for special purposes. All statistical analysis in this paper were calculated at the 5% level of significance.

Determination of spawning

Echinoderms collected for the biomass estimation were used also for this purpose. The determinations were done on preserved specimens.

Three of the species were sexed. For some species of echinoderms, it is possible to determine the sex directly by the colour of the gonads when they are ripe (Hyman 1955, Taylor 1958). The gonads of female Ophiura albida are green, while the male ones are orange, pink or white. The gonads of female Ophiura texturata are orange-red, while those of males are yellow or white. For Asterias rubens the length of one of the gonads was measured on 20-30 specimens in each of ten samplings. The mean gonad index was calculated as the ratio of gonad length to arm length multiplied by 100. For O. texturata and O. albida the specimens were classified as unripe, ripe, or spawned. Gonads which only filled a small part of the bursae and were small and firm, were said to be unripe. If the gonads filled the greater part of the bursae, were big and swollen, and contained eggs or sperm, they were said to be ripe. Gonads which were shrunken or contained only a residue of ripe eggs, were said to have spawned. Since only preserved animals were examined, no attempts were made to measure the size of the eggs.

According to Vevers (1949) the spawning time is better determined by studying the ripening of the gonads than the occurrence of larvae in the water. The reason for this is that the drifting of larvae from

neighbouring areas will introduce error.

Measuring the size

The animals were measured after they had been preserved in alcohol. For A. rubens the longest arm was measured by a divider on the oral side from the centre of the mouth. In correspondence with the accuracy of the method, the animals were divided into groups by their size, one group for every 5 mm interval. Vevers (1949) found that the arms of A. rubens were approximately 5 mm shorter after having been preserved in alcohol. The size of O. texturata and O. albida is usually given as the length of the disc diameter. Due to the great accuracy in the measurement of these rigid animals, size groups of 1 mm are used.

Stomach analysis

The material for the stomach analysis was preserved in 70% alcohol as soon as possible after sampling. Only adults of O. texturata and O. albida were examined. The range of size of the disc diameter was respectively 18-22 mm and 9-11 mm. The stomach was investigated by cutting off the dorsal half of the disc and examining the contents under a microscope (Taylor 1958).

Food investigations based on stomach content will tend to underestimate softbodied animal prey, and overestimate shelled animals such as molluscs. Besides, the results will depend on the amount of time it takes from sampling until the material is preserved. Diving was found to be more advantageous than the use of grab or trawl, because no washing had to be done after the sampling.

Estimation of biomass

The quantitative sampling was done on the seven transects (Fig. 2). Landmarks and buoys were used in order to locate the stations. Sampling was carried out using SCUBA-equipment. Diving was found to be a better quantitative method of collecting echinoderms than the use of

a Petersen grab. Especially the larger animals as A. rubens are underestimated by using the grab, probably because of the smaller sampling area (Skjæveland 1972).

Alle the echinoderms inside two 0.5 m² frames were picked up at each station. The frames were dropped randomly at 4, 8, 12, and 16 m depth along the transects. The depths were determined according to mean tide level and found by sounding with a leadline and controlled with a pressure recording depth gauge. The echinoderms inside each frame were put into a nylon bag and brought in sea water to the laboratory. The material was then preserved in 70% alcohol and stored for about a fortnight.

At intervals of approximately one month, 13 times in all, samples were taken from the transects. Sampling was done twice in June. No sampling was carried out in December and February. In January, March, and April the ice cover in the inner basin prevented sampling at transect 7, and at transect 6 in January. Because of practical difficulties, no sampling was done at transect 3 at 12 and 16 m in November, and at 16 m in January and March. This gives a total of 688 samples, each of 0.5 m².

The number of specimens of each species in each sample were counted. The total alcohol weight of all specimens of each species in the same sample was determined after the material had been allowed to dry on a blotting-paper for 10 min. The arms of the two species O. texturata and O. albida were easily broken during the collecting. A mean weight of an arm and half an arm for each of the two species was therefore determined (Table 1). These weights were added to the alcohol weights of animals with broken arms. This was done only for specimens with a disc diameter exceeding 7 mm.

Table 1. Mean alcohol weight in grams per arm and half an arm of Ophiura texturata and Ophiura albida. n = number of measurings

Species	n	arm	half arm
<u>Ophiura texturata</u>	44	0.549	0.184
<u>Ophiura albida</u>	81	0.205	0.044

Table 2. Mean dry weight in grams (d) of the organic matter dissolved in alcohol per gram alcohol weight (W) of the animals. n = number of measurements

Species	n	d
<u>Thyonidium pellucidum</u>	2	0.035
<u>Strongylocentrotus droebachiensis</u>	25	0.005
<u>Astropecten irregularis</u>	19	0.010
<u>Crossaster papposus</u>	2	0.020
<u>Henricia scabrior</u>	2	0.020
<u>Asterias rubens</u>	32	0.015
<u>Ophiopholis aculeata</u>	19	0.006
<u>Ophiura texturata</u>	29	0.004
<u>Ophiura albida</u>	30	0.004
<u>Ophiura robusta</u>	6	0.004

Some organic matter will dissolve in alcohol during preservation. For ten of the echinoderm species mean dry weights of dissolved organic matter per gram alcohol weight were determined (Table 2).

The use of dry weights is recommended for biomass estimations (Sanders 1956, Thorson 1957). Formulas for transferring alcohol weight to dry weight were obtained for ten of the species by measuring corresponding values of dry weight and alcohol weight of selected individuals of each species and determining the ratio between the two weights. The dry weight was found after decalcification, filtering, and drying as described by Holme (1953).

For species with about 20 pairs of data of dry weight and alcohol weight, a linear factor was calculated by means of linear regression analysis (Table 3). Second degree coefficients were also calculated by second degree regression analysis (Table 3). This last method was found to be markedly better only for A. rubens.

To the estimated dry weight of the transect material was added the calculated dry weight of organic matter dissolved in the alcohol. With the same symbols as in Tables 2 and 3, the formula used for dry weight determination of A. rubens is: $D = Wa^2 + Wb + Wd$. For the other species

Table 3. Factors calculated for transferring alcohol weight to dry weight. n = number of measurements, k = linear factor, SD(k) = standard deviation of k, b = first degree coefficient, a = second degree coefficient

Species	n	k	SD(k)	b	a
<u>Thyonidium pellucidum</u>	2	0.085			
<u>Strongylocentrotus droebachiensis</u>	25	0.054	0.002	0.041	0.0006
<u>Astropecten irregularis</u>	19	0.096	0.021	0.137	-0.013
<u>Crossaster papposus</u>	2	0.143			
<u>Henricia scabrior</u>	2	0.037			
<u>Asterias rubens</u>	35	0.134	0.005	0.092	0.003
<u>Ophiopholis aculeata</u>	19	0.103	0.004	0.092	0.008
<u>Ophiura texturata</u>	29	0.057	0.003	0.072	-0.007
<u>Ophiura albida</u>	30	0.038	0.003	0.038	0.0004
<u>Ophiura robusta</u>	6	0.087			

in Table 3 the formula is: $D = Wk + Wd$. No factors were calculated for the remaining species of the transect material, but Cucumaria frondosa was treated like Thyonidium pellucidum, Ophiura sarsi as O. albida, Amphiura chiajei and Amphipholis squamata as Ophiura robusta. For Leptasterias muelleri the linear coefficient of A. rubens was used.

Attempts were made to estimate errors in the dry weight due to the transformation process from alcohol weight. The error introduced by the inaccuracy in time when determining the alcohol weights was found to be negligible (Skjæveland 1972). These determinations will largely depend on the size of the animals (Brun 1969). The error in the dry weight determination of the organic matter dissolved in alcohol was computed for five of the species. This error was only a few per cent of the error due to the estimation of the linear factor k (Skjæveland 1972). An estimation of the error in the transformation from alcohol weight to dry weight can therefore be given, neglecting the dissolved organic matter, as a confidence interval CI(D) (Appendix I):

$$CI(D) = t_{n-1, \frac{\alpha}{2}} \sigma \left\{ 1 + \left[\frac{(D/k)^2}{\sum_{i=1}^n W_i^2} \right] \right\}^{\frac{1}{2}} \quad \text{where } t_{n-1, \frac{\alpha}{2}} \text{ is the}$$

table value of Students t test with $n-1$ degrees of freedom and significance level α . σ is the estimated standard deviation of the dry weight and is supposed to be the same for every dry weight value. n is the number of measurements in the calculation of k . W_1 is the measured alcohol weight used to calculate k . An illustration of the order of magnitude of the confidence interval is given in Table 4.

The order of magnitude of the linear coefficients in transferring alcohol weights to dry weights given in Table 3 is in close correspondence with those calculated by Petersen & Boysen Jensen (1911), Struve & Kairies (1930), Lee (1951), Holme (1953), and Lie (1968), when the various methods of weight determination are taken into consideration.

Table 4. Estimation of errors in the transformation of alcohol weights to dry weights. D = chosen values for the dry weight in grams, CI(D) = confidence interval in grams calculated from the formula p. 12

Species	D	CI(D)
<u>Strongylocentrotus droebachiensis</u>	1.50	0.47
<u>Astropecten irregularis</u>	0.60	0.51
<u>Asterias rubens</u>	4.50	0.58
<u>Ophiopholis aculeata</u>	0.10	0.05
<u>Ophiura texturata</u>	0.15	0.06
<u>Ophiura albida</u>	0.02	0.01

QUALITATIVE PART

The following echinoderms were found in the Borgenfjord area during the investigation period from autumn 1967 to autumn 1971 (species marked with an asterix are only found on stations just outside Borgenfjorden):

Holothuroidea: Cucumaria frondosa (Gunnerus), *Cucumaria elongata Düben & Koren, Cucumaria hvdmani (Thompson), *Thyone raphanus Düben & Koren, Thyonidium pellucidum (Fleming), Psolus phantapus (Strussenfelt).

Echinoidea: Strongylocentrotus droebachiensis (O. F. Müller), Echinocardium cordatum (Pennant).

Asteroidea: *Ctenodiscus crispatus (Retzius), Astropecten irregularis (Pennant), Crossaster papposus (L.), Henricia scabrior Heding, Asterias rubens L., Leptasterias muelleri (M. Sars).

Ophiuroidea: Amphiura chiajei Forbes, Amphiura filiformis (O. F. Müller), Amphipholis squamata (D. Chiaje), Ophiopholis aculeata (L.), Ophiothrix fragilis (Abildgaard), Ophiocomina nigra (Abildgaard), Ophiura texturata (Lamarck), Ophiura sarsi Lütken, Ophiura albida Forbes, Ophiura robusta Ayres, Ophiura affinis Lütken.

Occurrence of the species

The occurrence of the echinoderms in Borgenfjorden (Table 5) is determined by sampling both by using grab and diving. Sampling with a Petersen 0.1 m² grab was done on about 150 stations in July 1968 (Borgenfjordundersökelsene 1969). From August 1969 samples were normally taken with intervals of one or two months at the same 11 selected stations (Lande 1970).

At two localities, outside Borgenfjorden and on the Bosnes threshold, sampling was carried out only with the grab (Table 5).

The occurrence of the species in the transect material has been determined (Table 6). Ophiura albida is the most common species in the area (Table 5 and 6). This species also has a relative high density

Table 5. The occurrence of echinoderm species in four parts of the Borgenfjord area. =====; occurrence in more than 30% of the samples. ———; occurrence in 30-5% of the samples. -----; occurrence in less than 5% of the samples. Species marked with an asterix * are not represented in the transect material

Species	Borgenfjorden			
	Outside Strømmen	Outer basin	Bosnes threshold	Inner basin
<u>Cucumaria frondosa</u>		-----		
* <u>Cucumaria elongata</u>	-----			
* <u>Cucumaria hyndmani</u>		-----		
* <u>Thyone raphanus</u>	-----			
<u>Thyonidium pellucidum</u>	-----	-----	-----	
* <u>Psolus phantapus</u>	-----	-----	-----	-----
<u>Strongylocentrotus droebachiensis</u>	-----	-----	-----	-----
* <u>Echinocardium cordatum</u>	-----	-----		
* <u>Ctenodiscus crispatus</u>	-----			
<u>Astropecten irregularis</u>	-----	-----	-----	-----
<u>Crossaster papposus</u>		-----		
<u>Henricia scabrior</u>		-----		
<u>Asterias rubens</u>	-----	=====	-----	=====
<u>Leptasterias muelleri</u>		-----	-----	-----
<u>Amphiura chiajei</u>	=====	-----		
* <u>Amphiura filiformis</u>	=====	-----	-----	
<u>Amphipholis squamata</u>	-----	-----	-----	
<u>Ophiopholis aculeata</u>	-----	-----	-----	-----
* <u>Ophiothrix fragilis</u>		-----		
* <u>Ophiocomina nigra</u>		-----		
<u>Ophiura texturata</u>	-----	-----	-----	-----
<u>Ophiura sarsi</u>	-----	-----		-----
<u>Ophiura albida</u>	=====	=====	=====	=====
<u>Ophiura robusta</u>	=====	-----	=====	-----
<u>Ophiura affinis</u>	-----	-----	-----	-----

Table 6. Per cent occurrence of eight of the most common echinoderm species in the samples from the transects. Total number of samples is 688

Species	% occurrence
<u>Strongylocentrotus droebachiensis</u>	8.0
<u>Astropecten irregularis</u>	3.6
<u>Asterias rubens</u>	70.8
<u>Leptasterias muelleri</u>	4.8
<u>Ophiopholis aculeata</u>	5.4
<u>Ophiura texturata</u>	23.0
<u>Ophiura albida</u>	75.7
<u>Ophiura robusta</u>	11.8

with about 20 individuals per m^2 . Maximum density is found to be 78 adult specimens per m^2 .

The density of Asterias rubens is highest in the transect material. This is probably due to the greater sampling area. A total of 344 specimens of A. rubens with armlength greater than 5 cm were taken on the transects in one year. Only four specimens were caught using the grab in the same period. Using the grab the estimated density was approximately one seventh of the estimated density found by diving. Maximum density of adults was found to be 48 specimens per m^2 , but the occurrence of this species is probably quite variable.

Ophiura texturata is the third most common echinoderm in Borgenfjorden. Probably because of the size of these animals few are represented in each sample. A maximal adult density is found to be 10 specimens per m^2 . Relatively few have been caught with a grab.

Association between the three most common species

I have chosen to use the expressions Dice (1945) constructed to evaluate the co-occurrence of two animal species, A and B. Let NA and NB denote the number of samples in which the two occur, and NAB the number of samples in which both occur. The coincidence index DC is then

given by $DC = 2NAB/(NA + NB)$, and the quotient $A/B = NAB/NA$ tells how strong A is associated to B. The greater the values are, the stronger is the association. The value of the coincidence index DC is said to be due to chance if the value of a χ^2 -test (one degree of freedom) is smaller than 3.84.

Table 7. Figures for the association coefficient A/B and B/A, and coincidence index DC. The χ^2 -test value is indicated by χ^2 . Significant values of CD are marked with an asterisk*. Total number of samples is 688

A	B	NA NB	NAB	B/A	A/B	CD	χ^2
<u>Asterias rubens</u>		487					
	<u>Ophiura texturata</u>	158	116	0.24	0.73	0.69	0.63
<u>Asterias rubens</u>		487					
	<u>Ophiura albida</u>	521	393	0.81	0.75	0.78*	27.48
<u>Ophiura texturata</u>		158					
	<u>Ophiura albida</u>	521	155	0.98	0.30	0.46*	54.99

Table 7 shows that A. rubens and O. albida are rather strongly associated. This is probably due to their high occurrence (Table 6) and that both species are common on all sorts of substrate (Table 8). The coincidence index of O. texturata and O. albida is significant, but it shows no great association. The association coefficient B/A, however, indicates that O. albida is very likely to be found were O. texturata is present. O. texturata prefers soft bottom (Brun 1964), where also O. albida is very common. The coincidence index between A. rubens and O. texturata is not significant, and therefore the relative high value of the index probably is related to the randomness in the distribution of these rather large animals.

Substrate preference

The transect sample stations are divided into three kinds of substrate: hard, mixed, and soft bottom. Hard and mixed bottom is only represented on the transects in the outer basin. Because of the different

Table 8. Per cent occurrence of the three most common species on three kinds of bottom substrate. Outer and Inner = outer and inner basin. n = number of sample stations (0.5 m²) for each type of bottom

Species	Hard bottom	Mixed bottom	Soft bottom	
	n = 65	n = 78	Outer n = 78	Inner n = 88
<u>Asterias rubens</u>	98	90	86	73
<u>Ophiura texturata</u>	23	24	75	8
<u>Ophiura albida</u>	94	81	95	73

conditions, the two basins are treated separately with respect to the soft substrate. The values of Table 8 are tested with a χ^2 -test in order to show whether the occurrences on the various bottom types are evenly distributed or not. Significant difference was found for the soft bottom of outer and inner basin for O. albida but not for A. rubens. Furthermore, O. albida shows hard bottom preference, but only compared with mixed bottom. A. rubens shows hard bottom preference compared with soft bottom. All the same, Table 8 shows that these two species are common on all three kinds of bottom substrate. O. texturata shows highly significant soft bottom preference in the outer basin. According to Grieg (1913) and Brattström (1941) this species prefers muddy soft bottom and should therefore be more common in the inner than in the outer basin. It may therefore be assumed that other environmental factors differing between the two parts of the fjord are important. The results of Table 8 are in good agreement with what is usually found for these species according to Brun (1964).

Sex ratio

The sex ratio in the total transect material of A. rubens, O. albida, and O. texturata is shown in Table 9. If we assume that the sex ratio is 1, the expression $(\text{♀♀} - \text{♂♂})^2 / (\text{♀♀} + \text{♂♂})$ will have a χ^2 distribution with one degree of freedom. If the value of this expression exceeds 3.84, the ratio will be significantly different from 1 (Sverdrup 1964).

Table 9. Sex ratio for three species. Significant difference (marked with an asterix*) from 1 when $\chi^2 > 3,84$

Species	♀♀ + ♂♂	♀♀	♂♂	♀♀/♂♂	χ^2
<u>Asterias rubens</u>	258	144	114	1.26	3.49
<u>Ophiura texturata</u>	84	31	53	0.58	5.76*
<u>Ophiura albida</u>	1358	633	725	0.87	6.23*

Table 9 shows that the sex ratio of the two ophiuroids is significantly different from 1 with an excess of males for both. For A. rubens the value of the sex ratio is greater than 1. This indicates more females than males, but the value is not significant at the chosen level. Brun (1969) obtained the same result for this species in Manx waters, and Vevers (1952) for the Plymouth area with the sex ratio significantly greater than 1.

Correlation between the females and males of Ophiura albida

The purpose of calculating a correlation coefficient between the females and males is to see if the two sexes occur in equal numbers in the same area (0.5 m²). The sample size is large enough to justify the calculation of a monthly correlation coefficient. Furthermore, it is interesting to see if there is any variation in the correlation coefficient around the spawning time. For this species the period of spawning in Borgenfjorden in 1970 was found to be June-July (p. 21). Therefore, the transect material from March, May, June, and July is used in this examination (Table 10). Two correlation coefficients were calculated for each month, one for the total sampling area, and one for sampling areas where the sum of the specimens of O. albida exceeded seven.

There is a significant excess of males in March and May (Table 10). In these months the number of specimens of the sexes seems to be randomly distributed. In June and July the sex ratio is not different from 1 and the values of the correlation coefficients indicate that the two sexes are appearing in almost equal numbers in each unit area. This is particularly pronounced at the end of June at the same time as the spawning period starts (Table 12). This circumstance is probably one of the reasons why this species

Table 10. Sex ratio and correlation coefficients for *Ophiura albida* in spring 1970. Significant difference (marked with an asterix *) from 1 when $\chi^2 > 3.84$. N = the number of specimens per area of sampling (0.5 m²)

Date	♀♀+♂♂	♀♀	♂♂	♀♀/♂♂	χ^2	Correlation coefficient	
						All N	N > 7
17 - 19 March	262	105	157	0.67	10.32*	0.45	-0.12
11 - 13 May	217	94	123	0.76	3.88*	0.20	0.25
8 - 9 June	280	153	127	1.20	2.41	0.73	0.41
22 - 24 June	413	196	217	0.90	1.07	0.82	0.71
15 - 17 July	186	85	101	0.84	1.31	0.51	0.04

is so numerous in the fjord, because a behaviour like this should increase the possibility of successful fertilization.

Spawning period

Growth of gonads are usually measured by volume or weight increase (Boolootian 1966), but for *A. rubens* it can also be measured as an increase in length (Kowalski 1955), since growth will lead to a lengthening of the gonads as they are located in the arms. For *A. rubens* in Borgenfjorden the results of the growth of the gonads expressed as gonad index (ratio of gonad length to arm length x 100) are given in Table 11. Both sexes are treated together. The values from succeeding months are tested by Students t test in order to see if the two values are significantly different.

Table 11 shows that the growth of the gonads has taken place mainly from November to March. The decrease of the index in June, between 8 - 9 and 22 - 24, indicates that the majority of specimens spawn in the last half of June. A few specimens with arm length greater than 7 cm had spawned in May. A few ripe eggs were found in some of the gonads examined until the investigation was stopped in September. It is therefore reasonable to assume that spawning is going on over a relatively long period.

Table 11. Mean values of gonad index of Asterias rubens. Significant difference between succeeding values (marked with an asterix*) tested by Students t test. N = number of observations. GI = gonad index as ratio of gonad length to arm length x 100. SE = standard error of the gonad index. t = value of Students t test. T = table value of Students t test

Date	N	GI	SE	t	T
11 - 18 Oct. 1969	32	13.78	1.19	1.26	2.00
11 - 13 Nov.	32	16.10	1.41	7.20*	2.02
17 - 19 March 1970	20	45.96	4.76	0.47	2.04
14 - 16 April	19	43.52	1.79	1.01	2.00
12 - 15 May	46	38.73	2.98	0.49	2.00
8 - 9 June	16	35.83	5.25	2.96*	2.05
22 - 24 June	15	18.30	1.36	0.45	2.04
15 - 17 July	25	17.19	1.51	0.49	2.02
19 - 20 Aug.	22	16.00	1.99	1.80	2.02
28 - 29 Sept.	29	22.16	2.58		

The bigger animals show a tendency to spawn first. Only one specimen with arm length less than 5 cm had spawned during spring and summer, while several had spawned during August and September. The minimum length of the arm of a spawned specimen was 4.4 cm.

The results of the examinations of the gonads of the two ophiuroid species are given in Table 12. Both sexes are treated together. Ripe gonads in O. texturata were not found until May. Spawning did not occur until July 1970, and spawning was still taking place as late as in November 1970. As no sampling was performed after that time, it is impossible to give any further information about the duration of the spawning period of this species.

In contrast to O. texturata, the spawning period of O. albida seems to be short, from the beginning of June to about the middle of July. In spite of the large sample investigated, no ripe specimens were found in August and September, and it is reasonable to assume

Table 12. Numerical distribution of unripe, ripe, and spawned specimens of the total number (N) of examined individuals of Ophiura texturata and Ophiura albida in 1970

Date	N	Unripe	Ripe	Spawned
<u>Ophiura texturata</u>				
11 - 13 May	36	13	23	0
8 - 9 June	14	0	14	0
22 - 24 June	13	2	11	0
15 - 17 July	20	3	9	8
19 - 20 Aug.	25	3	9	13
28 Sept.	13	0	6	7
10 Nov.	38	16	13	9
<u>Ophiura albida</u>				
11 - 13 May	290	22	268	0
8 - 9 June	339	40	293	6
22 - 24 June	552	148	399	5
15 - 17 July	582	161	160	261
19 - 20 Aug.	1080	750	0	328
28 Sept.	269	162	0	107

that no spawning took place during these months. In winter and spring 1970 the gonads of O. albida were small and firm. Unripe specimens were found during the period of investigation. These were usually small, with a disc diameter of less than 7 mm. Ripe individuals always had a disc diameter greater than 7 mm.

For these three species the spawning in Borgenfjorden starts as the temperature is rising or is at its maximum value, for A. rubens at about 9°C, O. albida at about 12°C, and O. texturata at about 16°C. According to Orton (1920), spawning is usually connected to temperature limits which are fixed for the various species. Observations on spawning of these three species from other areas, give other temperature limits than those found in Borgenfjorden in 1970. For example: A. rubens spawns at Plymouth at 10-13°C (Vevers 1949), in the North Sea at 2-10°C, and in

the Baltic Sea at 10-16°C (Kowalski 1955). The spawning of these species usually takes place at a rising or a maximum temperature of the area. Exceptions are A. rubens in the North Sea (Kowalski 1955), and O. albida outside Bergen (Olsen 1943) where spawning was observed at the lowest temperature.

A closer correlation was found regarding the spawning period of echinoderms (Boolootian 1966). For the three species concerned, available information on spawning gives a maximum spawning period for A. rubens from February to July; for O. texturata from June to September, and for O. albida from April to September. This is in relatively good agreement with what was found in Borgenfjorden. Boolootian (1966) states that a single parameter that initiates the spawning has yet to be demonstrated. He has found no correlation between spawning and temperature for echinoderms except that the spawning period is lengthened at higher temperatures. The same effect is found for low salinity (Schlieper 1957). Besides, low salinity may cause the sperm cells to be inactive (Thorson 1946). The salinity is not any critical factor for these species in Borgenfjorden, because the salinity during spawning is at a minimum value, approximately 25^o/oo.

Quantitatively, increase of phytoplankton is considered an important factor in starting the spawning for animals with planktotrophic larvae (Thorson 1946). From April to October 1970 the phytoplankton occurred in great abundance in Borgenfjorden. November showed a typical winter situation with little phytoplankton (Sakshaug, pers. comm.). Of the three species, only A. rubens begins the spawning so early in the spring that it can be correlated with the increase of phytoplankton. The two ophiuroid species begin spawning when the quantity of phytoplankton has passed its maximum value. The larvae of these species appear in the pelagic while the food supply is rich, except for the latest broods of O. texturata.

Size distribution

Figs. 4, 5, and 6 show the size distribution of the three species. The smaller animals of A. rubens are by far the most common in the collected material. The juveniles were usually found on vegetation, especially on Laminaria sa charina (L.) Lamour. Monthly observations of the size distribution show that the juvenile asteroids with an arm length

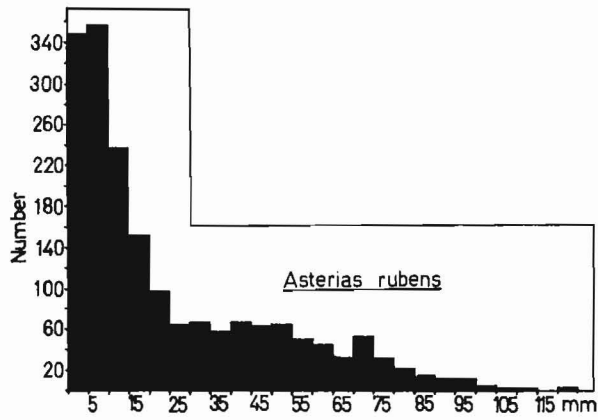
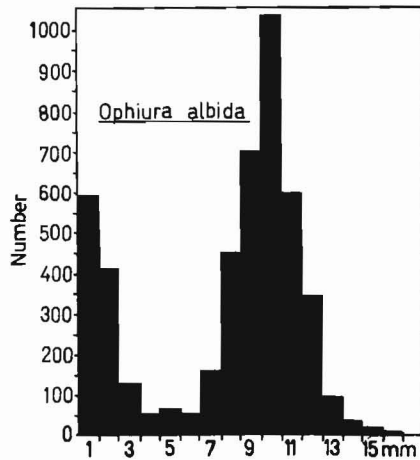
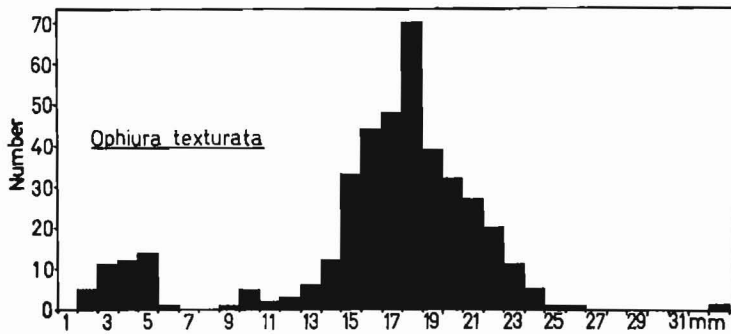


Fig. 4. The size distribution (longest arm in mm) of *Asterias rubens* in the transect material from July 1969 to September 1970.



Figs. 5 and 6. The size distribution (disc diameter in mm) of *Ophiura texturata* and *Ophiura albida* in the grab and transect material from July 1969 to October 1970.

less than 10 mm were most frequent in early September 1969 and late August 1970.

Juveniles of O. texturata were not found, or could not be distinguished from juveniles of O. albida. It is evident that at least two year-classes are represented in the material (Fig. 5). Monthly observations did not give any further information on growth or number of year-classes.

Almost the same picture is shown by the size distribution of O. albida. Because this species is the most common one, the ratio of the number of the two ophiuroids being 15/1 both for the transect material and the grab material (Skjæveland 1972), the juveniles found are assumed to be O. albida. At least two year-classes can be recognized in Fig. 6. Results of monthly observations showed that juveniles with a 1 mm disc diameter appeared in the material in great numbers in June 1970 and that juveniles with a 2 mm disc diameter were dominant in September 1970.

The lack of information on growth from the size distributions is probably due to the small number of specimens in some size groups, the sampling methods, and the relatively long spawning period for some of the species.

According to Mead (1901), Vevers (1949), Hancock (1958) the growth of A. rubens depends strongly on food supply. Investigations have shown that juvenile specimens prefer balanoids (Barnes & Powell 1951, Hancock 1955, 1958) and bivalvs later on (Petersen & Boysen Jensen 1911, Hunt 1925, Mortensen 1927, Poulsen 1951, Hancock 1955). Benthos investigations in Borgenfjorden have shown that the food supply for this species ought to be rather good (Borgenfjordundersökelsene 1969, Lande 1970). Balanoids are frequently found on the vegetation together with the juvenile asteroids. Molluscs such as Modiolus modiolus (L.) are common on the hard bottom. In Borgenfjorden this asteroid is found to feed also on the ascidian Ciona intestinalis (L.) (Gulliksen & Skjæveland 1973).

Stomach content of Ophiura texturata and Ophiura albida

About 21% of the analyzed stomachs of O. texturata and 17% of O. albida contained animal or plant remains. A survey of three categories of stomach content: remains of prey, bottom material only, and empty

stomachs is given in Table 13.

Table 13. Classification of examined stomachs. N = total number. Empty = number of empty stomachs. Prey = number of stomachs containing animal prey. Bottom = number of stomachs containing bottom material only. M indicates the methods of collecting the material (A = Agassiz trawl, G = Petersen 0.1 m² grab, D = diving)

Month 1970	<u>Ophiura texturata</u>					<u>Ophiura albida</u>				
	M	N	Empty	Prey	Bottom	N	Empty	Prey	Bottom	M
Febr.	A	15	8	0	7	35	22	4	9	A
March						17	5	1	11	G
April	G	4	3	0	1	23	12	1	10	G
May	D	6	0	2	4	20	1	11	8	D
June	G	4	2	0	2	30	15	7	8	D
July	G	5	3	2	0	18	9	3	6	G
Aug.	G	11	7	1	3	23	12	0	11	G
Nov.	A	33	6	11	16	34	15	7	12	A
Sum		78	29	16	33	200	91	34	75	

The number of components found were grouped in the following way:

	<u>Ophiura texturata</u>	<u>Ophiura albida</u>
Rhizopods	18	20
Polychaets	2	1
Crustaceans	4	5
Ostracods	4	8
Molluscs	11	11
Plant remains	1	2

Some of the animal prey were possible to identify. In the stomach content of O. texturata the following animals were found: 1 Myriochele sp. ,

1 Pectinaria koreni Malmgren, 1 Euphausiacea, 1 Ennucula tenuis (Montagu), 2 Cardiidae indet, 2 Abra spp., 1 Musculus sp., 1 Corbula gibba (Olivia), and of O. albida: 1 P. koreni, 1 Mysidae, 7 Abra spp., 2 C. gibba, 1 Turritella communis Risso.

The stomach analysis seems to show that the two ophiuroid species take almost the same type of prey. The results are in good agreement with those of other works on this subject. But the conclusions vary from author to author. Some state that these animals are carnivorous (Eichelbaum 1910, Blegvad 1914, Hunt 1925, Hagmeier & Künne 1950, Thorson 1957). Others characterize them as carnivorous detritus feeders (Yonge 1954, Taylor 1958), or as detritus feeders which only occasionally take animal prey (Wintzell 1918).

The greater part of the molluscs and ostracods found in the stomachs contained mud, and the identifiable crustaceans were planktonic forms. Besides, almost all stomachs with animal prey also contained bottom material. These preliminary results from Borgenfjorden should therefore indicate that these animals are mainly detritus feeders.

Wintzell (1918) and Thorson (1957) have both found that some echinoderms have a resting period of about two months, beginning before and ending after the actual spawning, when they do not eat. This should have been valid for O. albida. In Borgenfjorden this species spawns in June-July (Table 12), and the results in Table 13 show that this species eats during the same period. Only half of the stomachs examined were empty. The same results were also found in April and August. Only adults were collected for stomach analysis (p. 9). It is therefore doubtful that there exists a resting period during spawning for this species in Borgenfjorden. In close agreement with the results of Taylor (1958), May was found to have the lowest percentage of empty stomachs.

Although it is difficult on the basis of this food analysis to characterize these ophiuroid species as carnivorous, they will, due to their high density, represent a danger for the newly settled larvae and juveniles of the benthic invertebrates, because they engulf bottom material.

QUANTITATIVE PART

Biomass estimation

Biomass may be defined as the quantity of organic substance in live organisms per unit surface area expressed in weight units (Thorson 1957). Dry weights only (p. 11) will be used in the biomass estimations here. When mean values are calculated from five or more single results, the standard error is computed. Student's t test was used to determine any significant differences between two mean values. As described (p. 10) the total alcohol weight of all the specimens of each species on each sampling unit was measured and the dry weight calculated. With this method it therefore was not possible to exclude from the total biomass the heaviest animals with dry weights of more than 0.2 g. This should be done, according to Holme (1953) and Sanders (1956), when biomass results from different regions are compared.

Seasonal variation in biomass

An average monthly biomass value was calculated for the whole area of Borgenfjorden (transects 1-7) (Table 14). The biomass values of the inner basin (transects 6-7) were rather low and stable, ranging from 1.79 to 0.14 g/m². Only the average values of the seven transects for each month are presented in Table 14.

Even if the monthly biomass values of the total transect material of the echinoderms varies from 1.92 to 18.43 g/m², there is no significant difference between any two of them. The reason for this is the high uncertainty in the estimations. The same is also true for the values of Asterias rubens and Ophiura texturata. For O. texturata, significant difference in the monthly biomass estimations was found only between September 1969 and January 1970. Significant differences in the monthly estimations of the biomass of Ophiura albida were found between some of the autumn and winter months on one hand (August 1969, November 1969, and September 1970) and most of the spring and summer months on the other. It is therefore possible to indicate a seasonal variation in the biomass values of O. albida, the biomass having greater values in spring and summer than in

Table 14. Mean biomass values of the seven transects \pm standard error in g/m^2 dry weight for the different months. Total = the total transect material of the echinoderms

Date	Total	<u>Asterias rubens</u>	<u>Ophiura texturata</u>	<u>Ophiura albida</u>
July-Aug. 1969	1.92 \pm 0.56	1.62 \pm 0.66	0.05 \pm 0.02	0.13 \pm 0.04
Sept.	2.82 \pm 0.95	1.93 \pm 0.71	0.16 \pm 0.05	0.27 \pm 0.05
Oct.	3.20 \pm 0.91	2.55 \pm 0.64	0.13 \pm 0.05	0.17 \pm 0.06
Nov.	4.66 \pm 1.30	4.20 \pm 1.18	0.07 \pm 0.03	0.13 \pm 0.004
Jan. 1970	5.29 \pm 1.11	4.40 \pm 1.13	0.04 \pm 0.01	0.29 \pm 0.04
March	11.94 \pm 6.82	10.83 \pm 6.75	0.06 \pm 0.02	0.30 \pm 0.03
April	5.59 \pm 1.43	4.64 \pm 1.48	0.13 \pm 0.05	0.38 \pm 0.02
May	5.09 \pm 3.04	4.64 \pm 3.03	0.14 \pm 0.06	0.26 \pm 0.03
June 9 - 10	4.53 \pm 3.01	4.03 \pm 2.97	0.05 \pm 0.02	0.23 \pm 0.05
June 22 - 24	18.43 \pm 13.87	17.65 \pm 13.81	0.05 \pm 0.03	0.51 \pm 0.08
July	3.12 \pm 1.16	1.35 \pm 0.37	0.08 \pm 0.03	0.25 \pm 0.02
Aug.	4.30 \pm 1.60	3.90 \pm 1.47	0.08 \pm 0.05	0.30 \pm 0.08
Sept.	7.84 \pm 4.17	7.33 \pm 4.24	0.05 \pm 0.04	0.10 \pm 0.05

autumn and winter. It must be remembered, however, that this is a result of only one year of investigation, and may not be valid as a general rule in Borgenfjorden.

The results presented in Table 14 therefore do not give any reason to believe in any seasonal variation in the biomass values of the total material of the echinoderms, or of the separate species. In regard to the English Channel outside Plymouth, Holme (1953) found that yearly variations in the values of the total biomass completely masked the seasonal variations.

Total biomass of the echinoderms

An average biomass value for the total area of Borgenfjorden was calculated by giving the single results, from each transect and month, the same weight. Average values of biomass were also calculated for the outer basin (transects 1-5), the inner basin (transects 6-7), and for the individual seven transects (Table 15).

Table 15. Mean values of biomass \pm standard error in dry weight of the total transect material of echinoderms from July 1969 to September 1970. n = number of single results for the calculation of the mean

Area	n	g/m ²
Borgenfjorden (transect 1-7)	87	6.09 \pm 1.34
Outer basin (transect 1-5)	65	7.83 \pm 1.73
Inner basin (transect 6-7)	22	0.67 \pm 0.16
Transect 1	13	4.84 \pm 0.69
" 2	13	14.50 \pm 7.50
" 3	13	4.18 \pm 1.93
" 4	13	10.33 \pm 3.82
" 5	13	5.84 \pm 1.32
" 6	12	0.52 \pm 0.16
" 7	10	0.85 \pm 0.29

The estimated biomass of the echinoderms in Borgenfjorden is rather high. The average values of transect 2 and 4 are especially high. This is mainly due to extraordinary numbers of specimens of A. rubens in the last half of June on transect 2 and in March on transect 4 (Fig. 9).

Very little data on biomass estimation of echinoderms from other areas is available. Only three relevant investigations will be mentioned here. Petersen & Boysen Jensen (1911) made an investigation in Limfjorden. From 15 stations sampled with a Petersen 0.1 m² grab, the dry weight of echinoderms was estimated at (0.73 \pm 0.18) g/m². A similar investigation was done by Petersen (1915) in Oslofjorden. I have transferred his wet weights to dry weights by means of the coefficients calculated by Petersen & Boysen Jensen (1911). Mean biomass values of echinoderms from 13 stations south of Dröbak are in this way estimated at (0.46 \pm 0.22) g/m², and from 15 stations north of Dröbak at (0.22 \pm 0.13) g/m².

Biomass estimations of samples from 20 stations with a Holmes scoop sampler in the English Channel outside Plymouth (Holme 1953) showed that as much as 64.4% of the total dry weight was due to

specimens heavier than 0.2 g dry weight. The biomass of the echinoderms was estimated at about 2 g/m².

The great differences between these biomass estimations and those from Borgenfjorden (Table 15), are probably due to the dissimilarities in sampling methods, primarily the size of the area sampled. In addition to the environmental conditions, the fauna compositions will also cause different biomass values. This will not be discussed in detail.

There appears to be a significant difference between the estimated biomass for the outer basin (transects 1-5), and the inner basin (transects 6-7) (Table 15). According to Thorson (1957) both production and biomass will decrease towards the inner parts of a fjord or a gulf. Since the inner basin is separated from the main fjord by two sills, it is therefore reasonable, even though the area is small, that this tendency is found in Borgenfjorden. The variations in the biomass from the outer basin to the inner basin must be considered relative to the effects of the Bosnes threshold (Fig. 2). The most remarkable differences in the hydrographic conditions are the thermocline and the anaerobic situation with formation of H₂S below the threshold level in summer and autumn. The mixing of the water in the last part of the autumn will therefore probably induce poisonous conditions in the whole water column. Since the mixing seems to take place yearly, the poisoning effect can not be disastrous for the animals. But the larvae, which are at the most sensitive stage of development (Thorson 1946), will presumably be influenced. This may result in weak recruitment, especially of species whose larvae appear in the plankton in the autumn. Another reason for weak recruitment of pelagic larvae in the inner basin is the relatively weak current across the Bosnes threshold. Both these conditions will have a diminishing effect on the biomass.

The temperature conditions are not the same for the two basins. The rise in temperature starts later in the inner basin than in the outer basin. This is particularly pronounced beneath the threshold level. Rise of temperature is positively correlated to growth (Kinne 1970), and will therefore affect, directly and indirectly by the increase in food supply, the biomass values of the echinoderms.

The substrate in most of the inner basin is rather soft, and there are relatively small areas of gravel and stones (Fig. 3). Therefore, the fauna will be more scarce here than in the outer basin,

with less animal prey for, for example, A. rubens. Because A. rubens plays a dominating part in the total biomass calculations of the echinoderms (Table 14), the soft substrate will be a relative important factor.

There is no significant difference between any two biomass values of the five transects of the outer basin, and of the two transects of the inner basin. The figures of Table 15 demonstrate that the two hard bottom transects, 2 and 4, have the highest uncertainty in the monthly sample results.

Variations in biomass in relation to depth

The distribution of the biomass of the transect material of the echinoderms in relation to the four depths, 4, 8, 12, and 16 m is shown in Table 16. The values given are average values of the monthly samples. The biomass values of Table 16 have been tested for significance (Table 17).

Table 16. Mean biomass \pm standard error in g/m² dry weight of the total transect material of echinoderms in relation to depth.
n = number of single values determining the mean values
(the same n both for 4 and 8 m depth)

Transects	4 m	n	8 m	n	12 m	n	16 m
1-7	10.02 \pm 1.82	87	5.23 \pm 0.32	86	4.80 \pm 0.34	84	3.96 \pm 0.40
1-5	13.17 \pm 2.86	65	7.31 \pm 0.16	64	6.28 \pm 0.54	62	4.80 \pm 0.48
6-7	0.56 \pm 0.18	22	1.10 \pm 0.37	22	0.52 \pm 0.08	22	0.30 \pm 0.16

The biomass of the four depths of each transect is shown in Fig. 7. The biomass of the three most common species at the four depths in the outer basin (transects 1-5), and the inner basin (transects 6-7) is shown in Fig. 8.

In the total material of echinoderms there are obviously distinct differences in the biomass between the outer and inner basin at all four depths. The biomass is largest at 8 m in the inner basin, but there

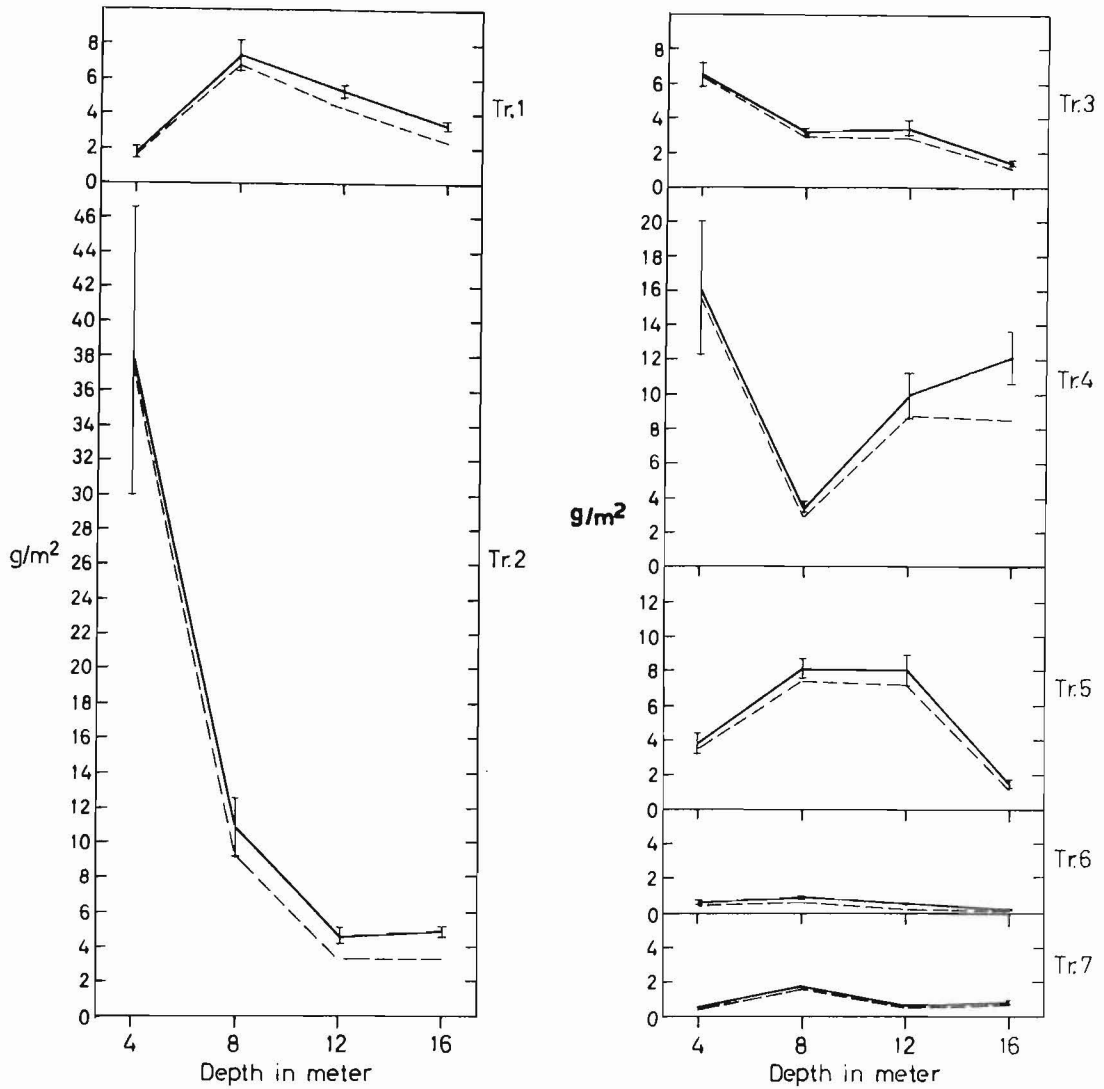


Fig. 7. Mean values of biomass as a function of depth on the seven transects for July 1969 to September 1970. Fully drawn line = total material of echinoderms. Vertical lines indicate standard error. Broken line = *Asterias rubens*.

Table 17. Calculated values of Students t test from the results of the biomass values in Table 16. Significant differences marked with an asterix *, Ts = table value of Students t test

Depths compared	Transects 1-7	Transects 1-5	Transects 6-7
4 and 8	2.60*	2.46*	1.31
8 and 12	0.94	1.85	1.55
12 and 16	2.42*	2.06*	1.22
8 and 16	3.43*	5.00*	1.97
Ts	1.96	1.98	2.02

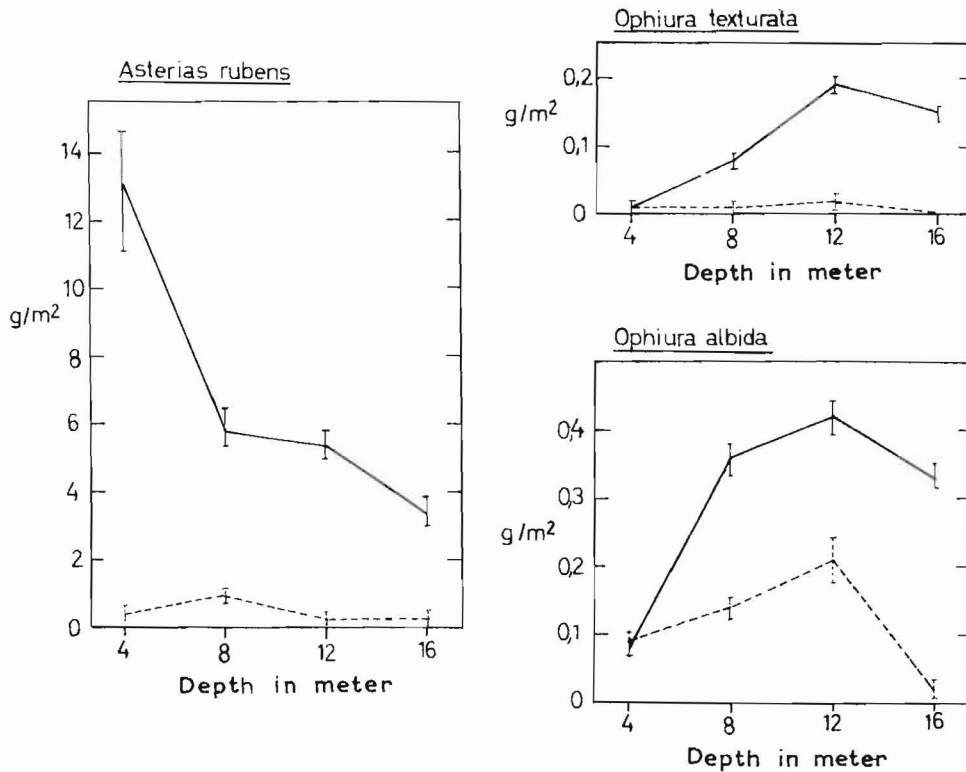


Fig. 8. Mean values of the biomass of the transect material of *Asterias rubens*, *Ophiura texturata*, and *Ophiura albida* as a function of depth from July 1969 to September 1970. Fully drawn line = mean of transects 1-5. Broken line = mean of transects 6-7. Standard errors are marked with vertical lines.

is no significant difference between any two depths (Table 17). The biomass usually decreases with depth (Spärck 1935, Thorson 1957). Gislén (1924) states that the biomass values of the shallow water forms are higher than those of the deep water forms within the same systematical group. The depth range in Borgenfjorden is too small to distinguish between shallow and deep water forms of echinoderms. The eight most common species are found at all depths, and the less common ones are too scarce to show any trends. Figs. 7 and 8 indicate clearly how strongly the biomass of the echinoderms depend on the weight of *A. rubens*, particularly at the 4 m depth in the outer basin, and especially on transects 2 and 4. Of the total biomass of *A. rubens* in the transect material, 61% have been taken at the 4 m depth. One of the reasons for this may be the rich epifauna on the hard

bottom transects. The current around Rolsøy, where these transects are located (Fig. 2) supplies good nourishment to various epifaunal elements which serve as food for A. rubens. The shallow water fauna is also rich because of the plant production which causes most of the herbivores to live here. The vegetation and the more variable substrate usually found here (Fig. 2) will give the animals hiding places.

The variation of the biomass with depth is not the same for each transect. Only transects 2 and 3 show the same trend as the total material (Fig. 7 and Table 16). On transect 4 the strong current, together with the steepness of the transect (Fig. 2), probably cause the low biomass values at 8 m. On this transect, the high biomass values at 16 m are partly due to Strongylocentrotus droebachiensis. This echinoid contributes 28% of the total dry weight of the echinoderms at this locality. Also on the deeper parts of transect 2 this species is relatively common. The biomass of the two ophiuroid species shows a relatively equal variation with depth (Fig. 8). The highest biomass values are found at 12 m, and the lowest at 4 m. This can be explained partly by the fact that these animals are supposed to behave with negative phototaxis (Fell 1966), and partly because of the soft bottom preference, especially by O. texturata (Table 8).

Biomass estimations of Asterias rubens, Ophiura texturata,
and Ophiura albida

In Figs. 9-11 are given the biomasses of the three species in g/m^2 from each of the four depths. Each column thus represents the total biomass of 4 m^2 , disregarding the few occasions when some of the depths were not sampled (p. 10). A black mark underneath the abscisse axis indicates that investigation was carried out without finding any animals.

Mean values of the biomass of the seven transects, and of the different parts of Borgenfjorden have been calculated (Table 18). The various results have been tested against each other in order to reveal any significant differences.

Table 18. Mean values of biomass \pm standard error in dry weight of Asterias rubens, Ophiura texturata, and Ophiura albida from July 1969 to September 1970. n = number of single values in determining the mean value

Transect	n	<u>Asterias rubens</u>	<u>Ophiura texturata</u>	<u>Ophiura albida</u>
1-7	87	5.13 \pm 2.59	0.08 \pm 0.01	0.24 \pm 0.02
1-5	65	6.95 \pm 1.67	0.11 \pm 0.014	0.30 \pm 0.02
6-7	22	0.54 \pm 0.16	0.01 \pm 0.006	0.12 \pm 0.03
1	13	3.66 \pm 0.53	0.14 \pm 0.02	0.36 \pm 0.02
2	13	13.50 \pm 7.49	0.09 \pm 0.03	0.37 \pm 0.07
3	13	3.74 \pm 0.91	0.16 \pm 0.03	0.22 \pm 0.03
4	13	8.84 \pm 3.91	0.03 \pm 0.02	0.24 \pm 0.04
5	13	5.01 \pm 1.27	0.12 \pm 0.04	0.29 \pm 0.08
6	12	0.33 \pm 0.17	0.01 \pm 0.006	0.18 \pm 0.05
7	10	0.80 \pm 0.25	0.01 \pm 0.003	0.03 \pm 0.01

Asterias rubens

The biomass values of this species vary greatly from one sample to another both from place to place, and from month to month (Figs. 9a and b). The mean values of each of the five transects in the outer basin show no significant differences although the values range from 3.66 to 13.50 g/m² (Table 18). The biomass values of A. rubens in the inner basin are rather low (Table 18), partly because of fewer individuals in the samples, and partly because of smaller weight per individual than in the outer basin. It is reasonable to believe that all the factors mentioned on p. 31-32 may explain the low values in biomass.

The importance of the food situation on the growth of A. rubens is discussed on p. 25. The variations in the biomass values of this species should therefore be compared with the available food supply on the spot. Such a comparison has been possible to do with the ascidian Ciona intestinalis because simultaneous sampling of this ascidian and A. rubens was carried out on the transect (Gulliksen 1971). On those localities where C. intestinalis was most abundant, especially on the upper part of transect 2, it was found that the biomass of A. rubens

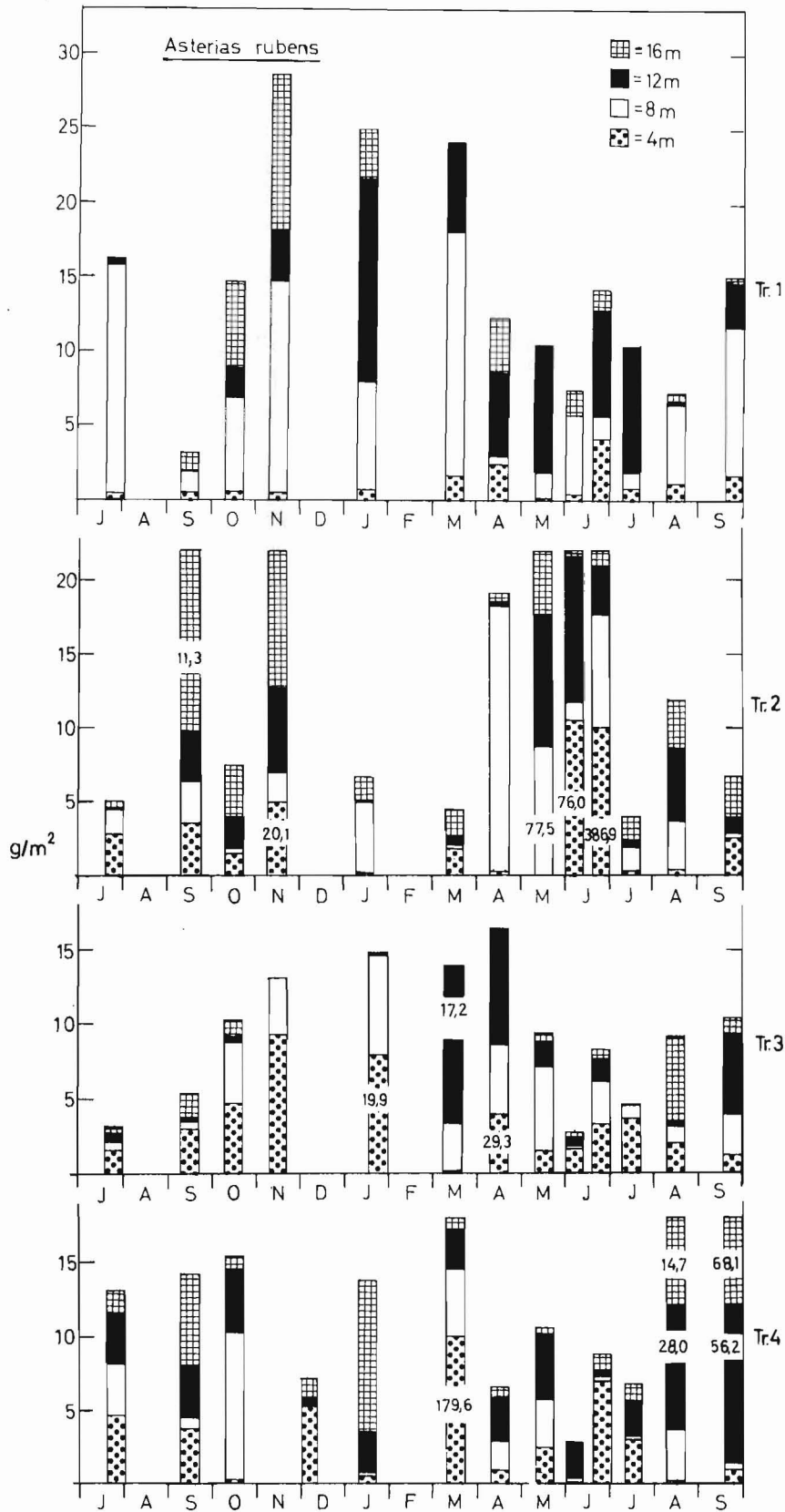


Fig. 9a. Biomass of *Asterias rubens* at transects 1-4 from July 1969 to September 1970.

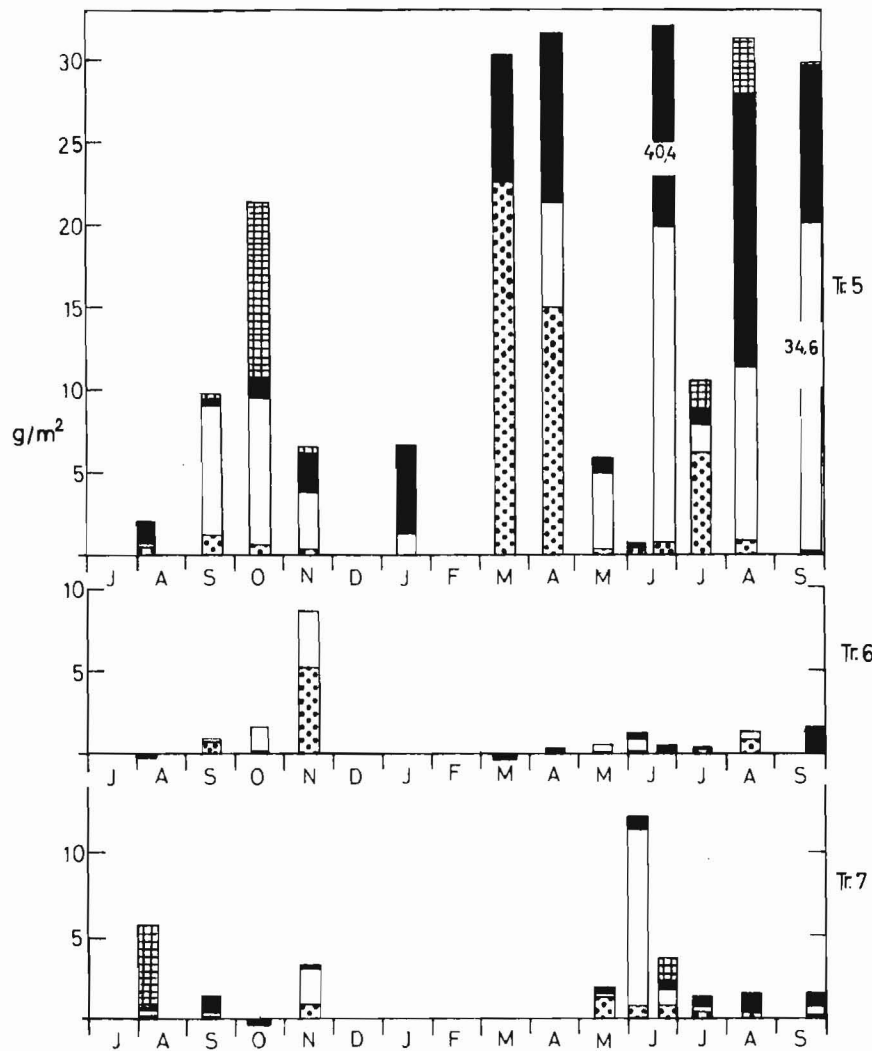


Fig 9b. Biomass of *Asterias rubens* at transects 5-7 from August 1969 to September 1970.

correlated with the biomass of the ascidian (Gulliksen & Skjæveland 1973). It is reasonable to believe that lack of available prey on the soft bottom of the inner basin is the main reason for the small biomass values of transects 6 and 7.

Ophiura texturata

Fig. 10 demonstrates that this species is most common at transects 1 and 3, but in the outer basin only the average values of transects 3 and 4 (Table 18) show significant differences. It is reasonable to assume

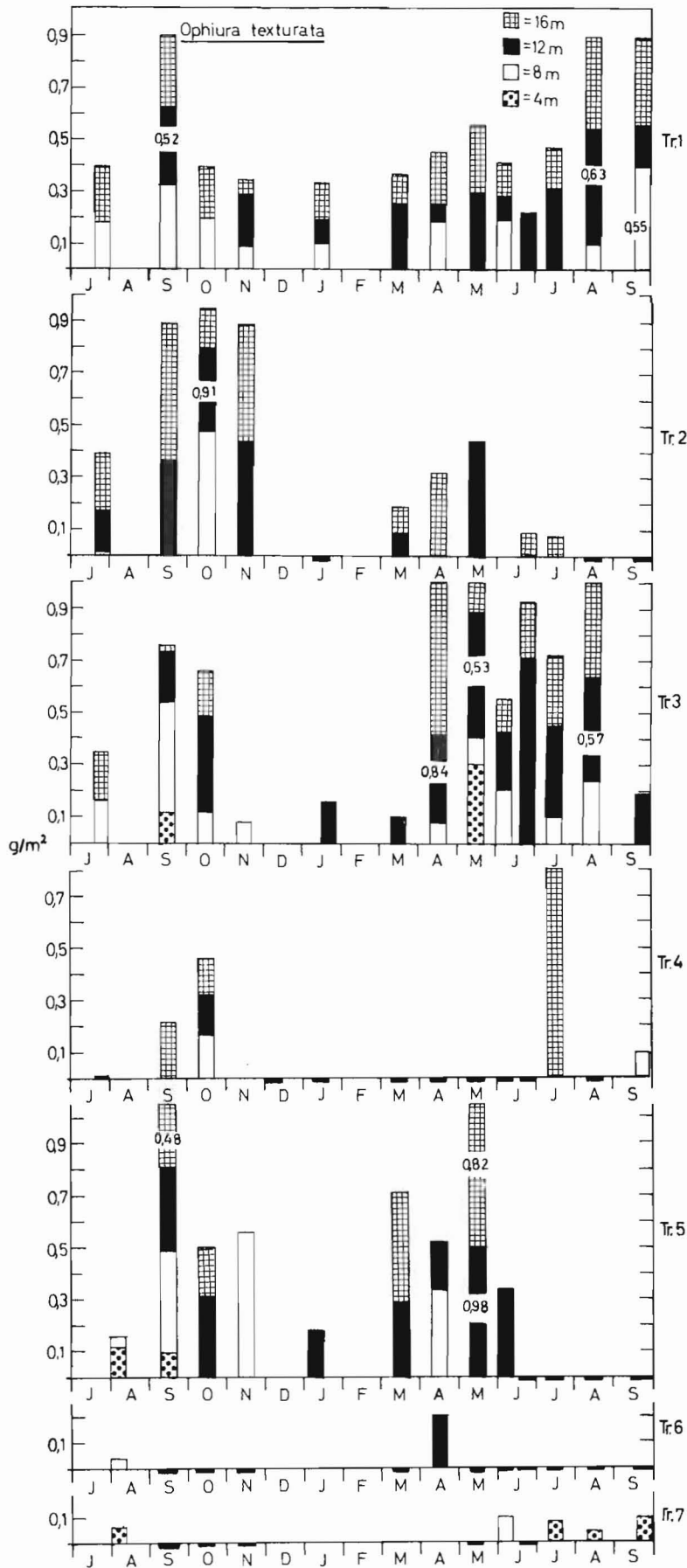


Fig. 10. Biomass of *Ophiura texturata* at transects 1-7 from July 1969 to September 1970.

that the distribution pattern of this species in the outer part of Borgenfjorden is caused by the soft substrate preference. The biomass values on the hard bottom transects (2 and 4) are relatively low, especially on transect 4. On transect 2 the substrate is softer towards the deeper parts. This is probably the reason for the relatively high values found here (Fig. 10).

The low biomass values on transects 6 and 7 (Table 18) are probably not caused by the substrate (p. 18). It is more likely that the low biomass values found here are related to the poisonous condition during the upwelling in the inner basin at the same time as the spawning of this species (Table 12), and the settlement of the larvae.

Ophiura albida

This species has almost the same average biomass values on all the five transects of the outer basin (Table 18). There is only significant difference between the values of transect 1 and the values of transects 3 and 4. A. rubens and O. albida are very well represented on all kinds of substrate (Table 8). Brattström (1941) showed that O. albida was

Table 19. Mean values \pm standard error of number of specimens and dry weight per specimen of Ophiura albida on 12 and 16 m (2 m^2) of the seven transects from July 1969 to September 1970. n = number of measurements for each mean value

Transect	n	number	weight in grams
1	13	63.9 \pm 5.0	0.017 \pm 0.001
2	13	43.1 \pm 5.7	0.025 \pm 0.005
3	12	30.4 \pm 5.0	0.020 \pm 0.010
4	13	24.0 \pm 5.3	0.018 \pm 0.010
5	13	27.1 \pm 7.4	0.018 \pm 0.012
6	12	18.5 \pm 4.3	0.019 \pm 0.020
7	10	0.2 \pm 0.01	0.001 \pm 0.003

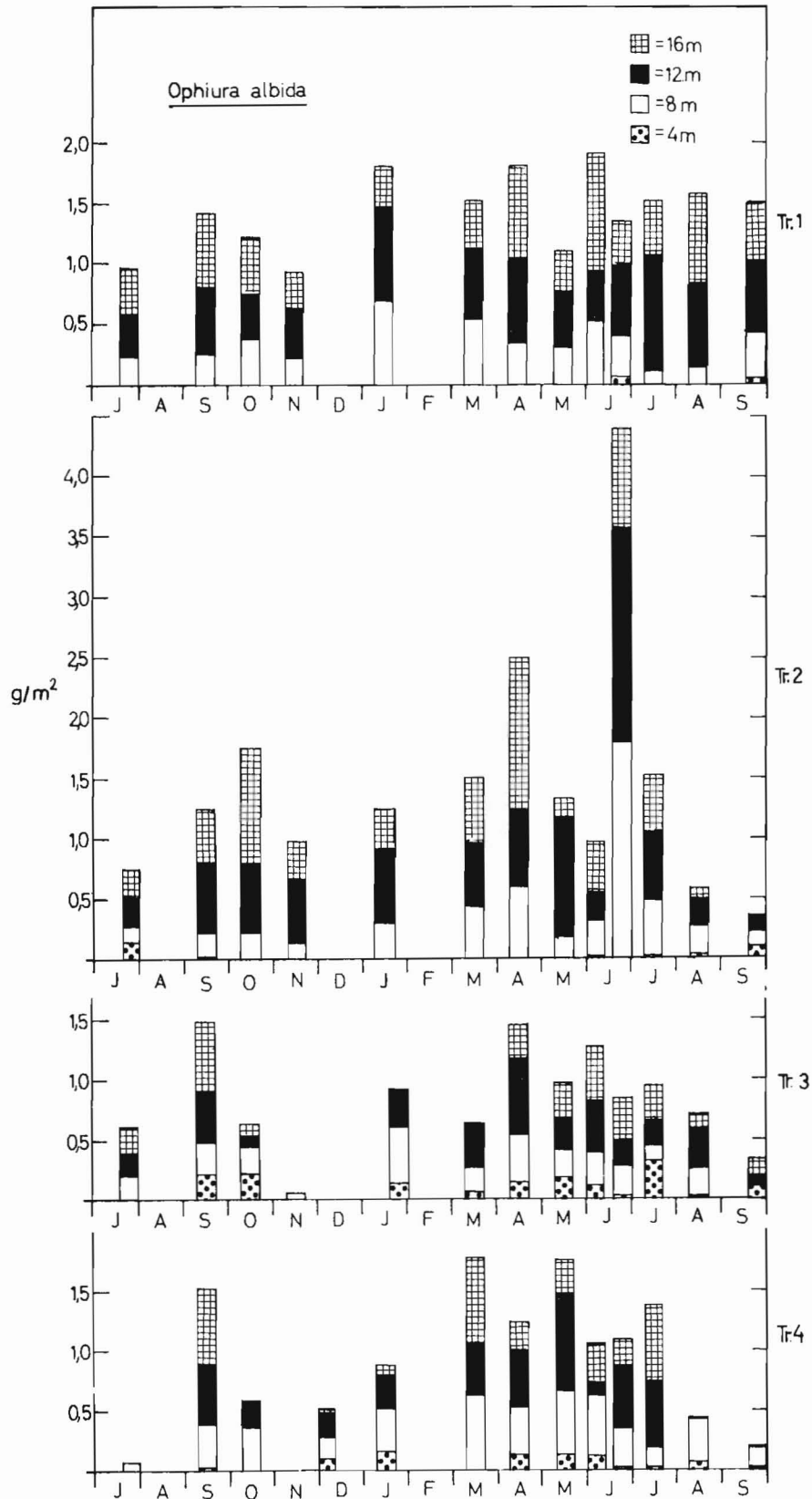


Fig. 11a. Biomass of Ophiura albida at transects 1-4 from July 1969 to September 1970.

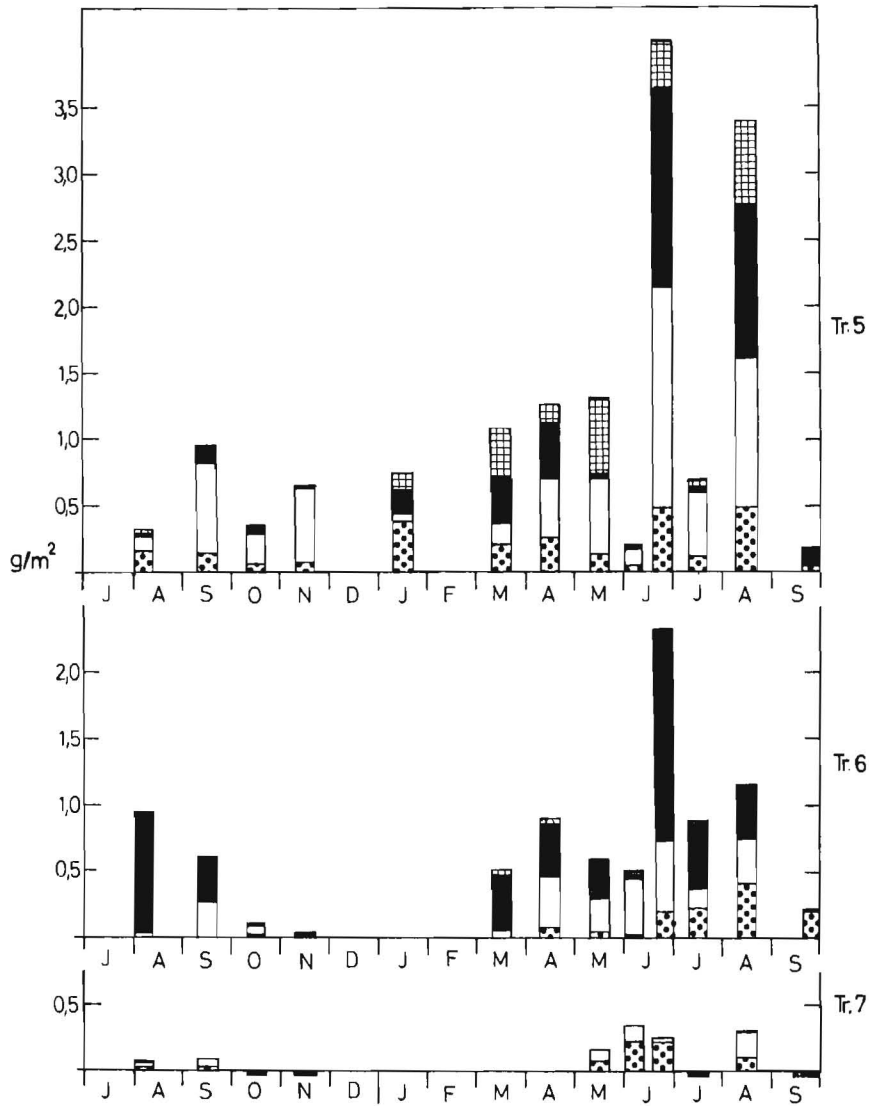


Fig. 11b. Biomass of *Ophiura albida* at transects 5-7 from August 1969 to September 1970.

most numerous on muddy bottom, but attained the greatest size on harder bottom types. In Borgenfjorden *O. albida* was very numerous on transect 1 at the 12 and 16 m depths (Table 19), but the mean weight per specimen was relatively low. Students t test shows significant difference both for the mean number and the mean dry weight per specimen between transects 1 and 2. On the same sample stations *O. texturata* also showed relatively stable and high biomass values throughout the year (Fig. 10). The low specimen weights of *O. albida* found here may therefore be due to intra-specific competition, since these two species are supposed to have almost the same diet (p. 27). The highest values of the mean specimen weight are

found on transect 2 (Table 19). This should indicate that the food situation is rather good at this locality. A couple of other species, Ophiura robusta (Skjæveland 1972), Ciona intestinalis (Gulliksen 1971), show high biomass values on this locality.

The biomass values of O. albida are relatively large on transect 6 compared with the other species (Table 18). This species was found four times at 16 m on transect 6 (Fig. 11b). These findings correspond to the high oxygen content of the bottom water. The biomass on this transect decreases starting in August. At the same time, the maximum values of biomass of this species moves from deeper to more shallow areas (Table 20). The results in Table 20 and Fig. 11b indicate that some of this species apparently migrates from transect 6 and moves away from the deeper parts during the period from August to November 1969. This is probably caused by the decrease in oxygen content on the bottom of the inner basin, and the poisoning effect in connection with the upwelling of water with H₂S late in the autumn.

Table 20. Biomass values of Ophiura albida in percentage of the total biomass at the four depths investigated. Results given are for each of the four samples at transect 6 in the autumn 1969. The numbers in the lowest row are the biomass values of Ophiura albida on the transect in percentage of the total biomass of this species of the four samples

Depth in meters	4 Aug.	18 Sept.	18 Oct.	12 Nov.
4	0	0	10.2	95.8
8	4.3	43.7	74.6	4.2
12	93.2	56.3	15.3	0
16	2.5	0	0	0
	54.5	37.1	7.0	1.4

On transect 7, the biomass values of O. albida are very small (Fig. 11b). Contrary to the situation in the outer basin, this species is most common at 4 and 8 m depth on transect 7. Anaerobic conditions

are not found at the bottom of the innermost part of the fjord, but due to the weak current, the low biomass values may be caused by lack of food. It is possible that O. albida may serve as prey for A. rubens especially on this locality where the fauna is rather scarce.

SUMMARY

1. The investigation was carried out in Borgenfjorden, a landlocked fjord in the inner part of Trondheimsfjorden (63°30' - 64°30'N, 9°30' - 11°30' E). Borgenfjorden, which is about 10 km long, is divided into two basins by a threshold. Anaerobic conditions are found during the summer and autumn beneath the thermocline (15 m) in the inner basin. The bottom substrate is primarily soft in this basin. The outer basin has almost the same hydrographic conditions in the entire water column (maximum depth 40 m). The type of bottom substrate varies. Temperature and salinity ranges during the investigation were 1.1 - 16.1°C and 24.8 - 33.9‰ respectively.
2. The echinoderm material in this investigation was collected mainly by diving on seven transect lines, two in the inner basin, and five in the outer basin. Samples were taken at 4, 8, 12, and 16 m depth along each transect. The sampling surface was two areas each of 0.5 m². Sampling was done from July 1969 to September 1970, 13 times in all, with intervals of about a month.

Sampling with a Petersen 0.1 m² grab was initiated in September 1967, and has been carried out primarily on 11 selected stations including one just outside Borgenfjorden.
3. A total of 25 species (six holothuroids, two echinoids, six asteroids, and 11 ophiuroids) were registered. Only 11 of these were found in the inner basin, and three were only found outside Borgenfjorden.
4. Derived conversion formulas for alcohol weight to dry weight have been used on 10 of the species.
5. The gonads in the three most common species were examined in order to determine the spawning period. Asterias rubens was found to spawn from May to September 1970, Ophiura texturata from July 1970 with spawning still taking place in November when this investigation was terminated, and Ophiura albida from July to August 1970. Correlation between females and males of O. albida was found to be greater in June than in March, May, and July.
6. The size distribution of the three most common species gives no basis for age or growth determinations.

Few specimens of A. rubens were observed with an arm length greater than 90 mm, and the majority of the specimens was less than 10-15 mm. The most numerous size groups of O. texturata and

- O. albida were those of 18 and 10 mm disc diameter respectively.
7. Stomach content examination for both O. texturata and O. albida showed fewest empty stomachs in May. The food consisted mainly of bottom material, some molluscs and crustaceans, but few polychaets. A resting period in connection with the spawning was not clearly observed.
 8. Average values of the biomass of the echinoderms in Borgenfjorden (transect material 344 m²) were estimated at (6.1 ± 1.3) g/m². Significant difference was found between the biomass values of the two basins, the outer with (7.8 ± 1.7) g/m² and the inner with (0.7 ± 0.2) g/m². The reason for this is thought to be the difference in the environmental conditions caused by the threshold.
 9. No seasonal variation in the biomass values was observed.
 10. The biomass variation with depth shows largest values at 4 m and smallest at 16 m. This fact is due to the biomass variation of the dominant species, A. rubens, which comprises 84% of the total biomass of the echinoderms in the transect material.
 11. The biomass values of O. albida decrease markedly downwards to that depth where anaerobic conditions are found in the inner basin (transect 6).

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APPENDIX I

Derivation of the confidence interval CI(D)

We denote the observations by $(D_1, W_1), (D_2, W_2), \dots, (D_n, W_n)$. Each D_i is a random variable corresponding to the given W_i . The following model is assumed:

$E(D_i) = k \cdot W_i$ and $\text{Var}(D_i) = \sigma^2$ for $i = 1, 2, \dots, n$. k is estimated by the method of least squares which gives

$$\hat{k} = \frac{\sum_{i=1}^n D_i \cdot W_i}{\sum_{i=1}^n W_i^2} \quad \text{and} \quad \text{Var}(\hat{k}) = \frac{\sigma^2}{\sum_{i=1}^n W_i^2}.$$

With this estimated value \hat{k} , the conversion formula from a given alcohol weight W to the estimated dry weight \hat{D} becomes $\hat{D} = \hat{k} \cdot W$, and $\text{Var}(\hat{D}) =$

$$W^2 \cdot \frac{\sigma^2}{\sum_{i=1}^n W_i^2}, \quad \text{with} \quad \text{Var}(D - \hat{D}) = \sigma^2 \cdot \left(1 + W^2 / \sum_{i=1}^n W_i^2\right).$$

The expression $R = (D - \hat{D}) / \sigma \cdot \left(1 + W^2 / \sum_{i=1}^n W_i^2\right)^{\frac{1}{2}}$ has a Students t

distribution with $n - 1$ degrees of freedom. If we put

$$P(-t_{n-1, \frac{\alpha}{2}} < R < t_{n-1, \frac{\alpha}{2}}) = 1 - \alpha \quad \text{where } \alpha \text{ is the level of significance and}$$

$t_{n-1, \frac{\alpha}{2}}$ is the table value of the Students t test, the confidence interval CI(D)

is given by

$$\hat{D} \pm t_{n-1, \frac{\alpha}{2}} \cdot \hat{\sigma} \cdot \left(1 + W^2 / \sum_{i=1}^n W_i^2\right)^{\frac{1}{2}} \quad \text{where} \quad \hat{\sigma}^2 = 1/(n-1) \cdot \sum_{i=1}^n (D_i - \hat{k} \cdot W_i)^2.$$

