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The Norway Lobster in Faeroe Waters

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CONTENTS

INTRODUCTION

This paper is based on field observations planned by Dr. phil. Å. Vedel Tåning, the late director of the Danish Institute for Fishery and Marine Research, and carried out mainly in 1937 (by Dr. Tåning and the author) and 1939 (by the author). The laboratory work (description of early stages, calculations, and preparation of tables and graphs) was planned and carried out by the author, partly in 1940, partly in 1959–1960 during the preparation of the manuscript, which was carried out on the initiative of Dr. phil. E. Bertelsen, director of the Danish Institute for Fishery and Marine Research, and made possible by a grant from "Statens almindelige Videnskabsfond". The morphological drawings were prepared by Mr. P. Winther.

METHOD

FISHING SHIP AND GEAR

In 1937 and 1939 the field work was carried out by an ordinary Danish fishing boat, M/C "Amy" (S. 109) of 31 gross register tons, and only a few observations mentioned in the paper were made from other vessels in other years.

The main gear was a "Norway Lobster Trawl", which may be described as follows:

The otterboard: 1.21 × 0.85 m
Meshes in wings: 45 mm
Meshes in belly: 38 mm
Meshes in cod-end (about 3 m from end): 34 mm
Foot rope, total: 39.5 m, of which 1.8 m between wings and, on each side, 1.4 m from wing to bar.
Head line: 32 m, of which 2.5 m between wings.
From end of cod-end to foot rope: 12 m.

MEASUREMENTS

Total length from the tip of the rostrum to the posterior edge of the telson (not counting the setae) was taken to nearest cm below by a measuring board, the *Nephrops* lying on its back with the tip of the rostrum against the headpiece. The length of the carapace was taken by a pair of compasses.

Weighing was carried out by an ordinary kitchen balance with a movable weight, the smallest unit being 2 g and the highest load 5 kg.

DISTRIBUTION AND ABUNDANCE

DISTRIBUTION

The map Fig. 1 shows the places where *Nephrops norvegicus* (L.) were caught during the present investigation, and Fig. 2 shows the places where the *Nephrops* trawl or a similar, but smaller mesh shrimp trawl has been used. The most important feature of the maps is the absence of the species from Suderø, although muddy bottom is present in the fjords (at Sandø the bottom is sandy and therefore not fit for *Nephrops*). In contrast to this the species is present at the northern islands in literally all the places where the bottom is mud.

ESTIMATION OF THE POPULATION BY CATCH PER UNIT EFFORT

The abundance was estimated in two ways, viz. by the catch per unit effort, which is an estimate of the density, and by marking, which gives an estimate of the size of the population in a certain place as well as the size of the area it occupies.

The density is illustrated by Table 1, which gives the weights of the catches. These weights were found in the following way:

1) As a rule the catch was sorted into large and undersized prawns according to a size limit of 16 cm. The large prawns were measured in boxes, a box being reckoned as 25 kg. Undersized and smaller quantities of large prawns were weighed by a steel yard.

2) In some cases some or all animals of a catch were weighed singly, and the weight of the catch was then calculated from these weights.

3) Often a full box of the unsorted catch was set aside to be measured. The weights of these were calculated from the mean weights (p. 294).

4) In 1939 parts of the catches were marked according to size and liberated, and the weights of these were also calculated from the mean weights (p. 294).

5) As the catch per hour is strongly influenced by the intensity of the light (cf. p. 320), it is not a good estimate of the abundance. However, the light also influences the percentage of large prawns, and the influence of the light may be estimated by means of this percentage. Using this information the estimated catch per hour in complete darkness has been calculated in the following way: On the graph Fig. 22 (p. 319) the theoretical altitude of the sun corresponding to the percentage of large prawns is read off, and by this figure the likely catch per hour in Kalbak Fjord is read off on the graph Fig. 23 (p. 320). The actual catch in question is then divided by this figure and multiplied by the maximum catch per hour in Kalbak Fjord.

This estimate is obviously a very rough one (cf. for one thing the deviations from the two graphs for Kalbak Fjord), but still it is better than the raw figures because the large deviations due to variations in the light are eliminated.

Judging the abundance by the catch per hour we get the following picture (for a detailed description of the bottom see Andersen 1940):

The best known area is the outer part of the Kalbak Fjord (depth: 30–57 m), because it is comparatively small and has been fished in two summers at almost any time of the day and night. The density of the population is illustrated by Fig. 23 (p. 320). The mean maximum catch per hour (in "complete" darkness) was 210 kg.

The area Sundene West of Fleserne is bigger and has a denser population north of Kællingen (1937, cf. Table 1) as well as south of it (1939); the mean maximum catches per hour were 299 kg, and 589 kg respectively. Thus the density was here about twice that of Kalbak Fjord, obviously because the depth was nearer to the optimum of the species, greater depth being associated with lower intensity of light and, therefore, more feeding hours for the younger individuals (see p. 319).

Also in Sundene north of the stream the population is more dense (298 kg/h) than in Kalbak Fjord in accordance with the somewhat greater depth.

In the inner part of Kalbak Fjord the density is lower (138 kg/h) corresponding to the smaller depth in most of the area and to the partly sandy bottom.

In most of the less well known places the density was found to be lower than in Kalbak Fjord, but this difference need not be real, because in many of the cases

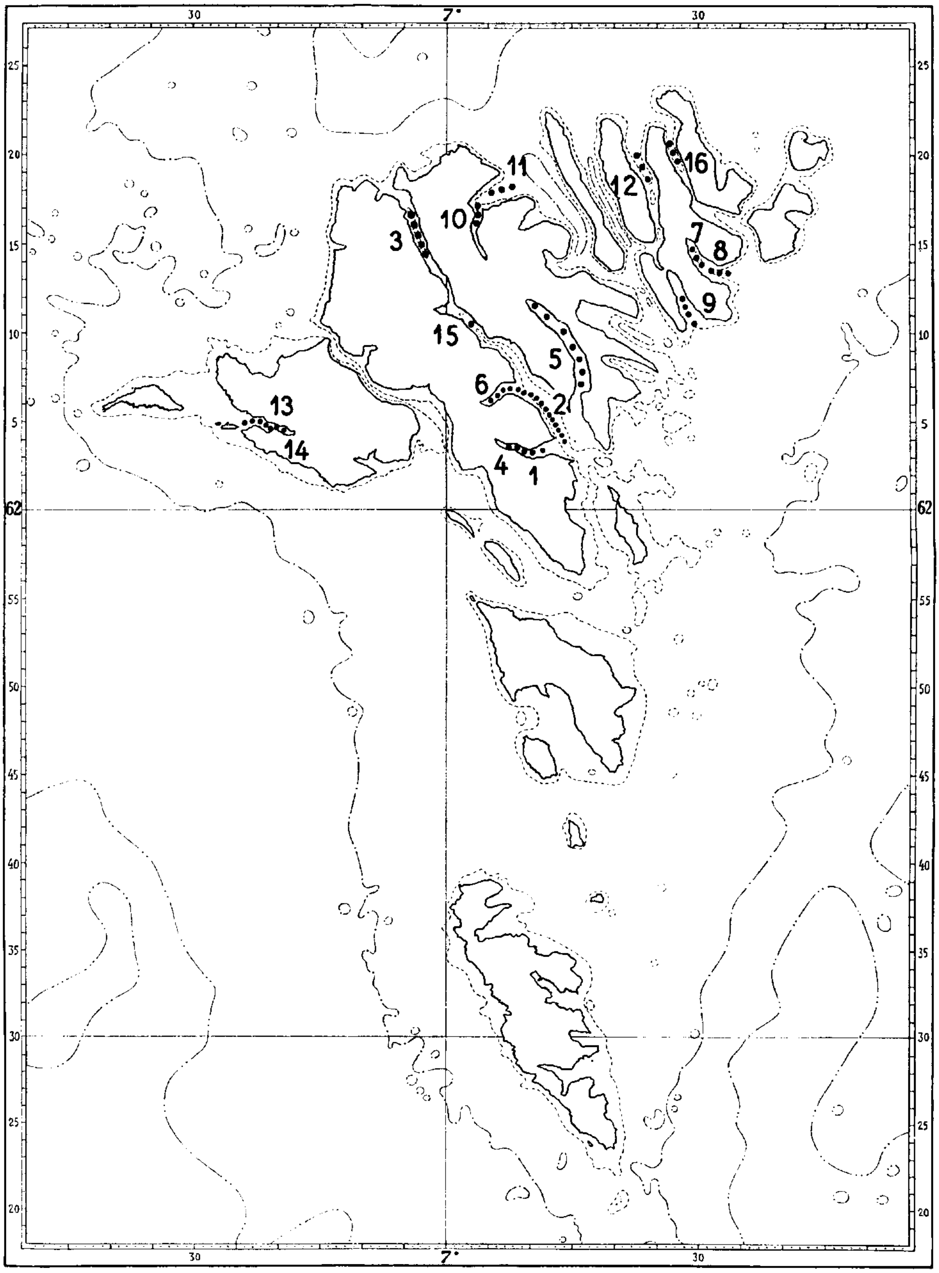

Fig. 1. Places where *Nephrops norvegicus* (L.) was caught in the trawl during the present investigation. The numbers refer to the list, Table 1 (outer part of Kalbak Fjord (1) is not in the list).

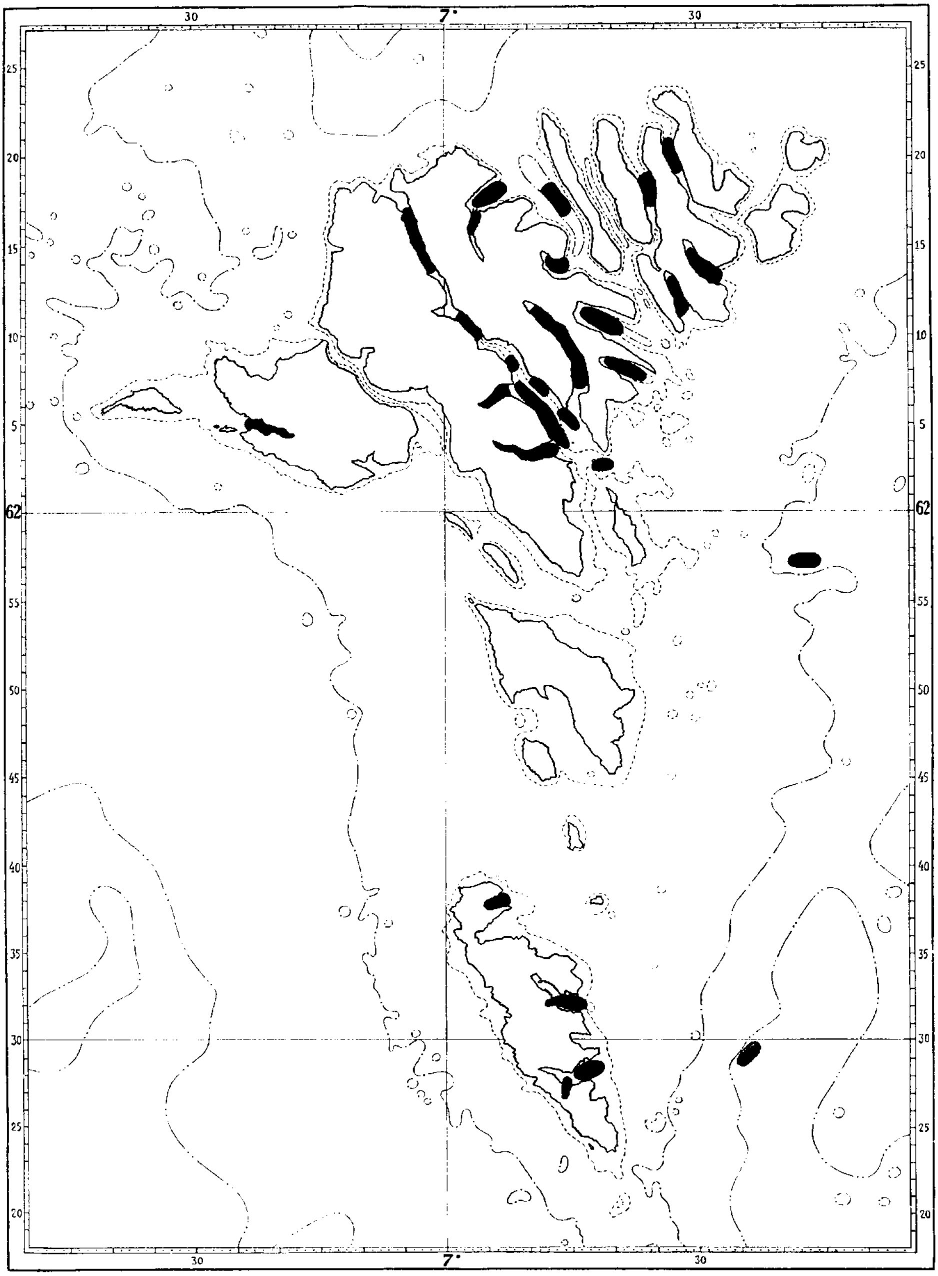

Fig. 2. Places where a "Norway Lobster Trawl" or a "Shrimp Trawl" has been used during the present investigation (cf. Andersen 1940).

Table 1.

List of catches of *Nephrops* in Faeroe waters 1937 and 1939 to show the density of the population. The numbers in brackets after the names of the localities refer to the map Fig. 1. Kalbak Fjord, outer part (1) is not included; the density in this fjord is illustrated by Fig. 23. In all cases but one, the gear was the "Norway Lobster Trawl". The four columns to the right concern the correction for the effect of the light (for explanation cf. the text p. 267).

Locality	Year	Date	Hour	Depth (m)	Duration of hauls (minutes)	Catch (kg) Total	Catch (kg) Large (≥ 16 cm)	Catch per hour (total)	Weightpercentage of large prawns (≥ 16 cm)	Light index	Corresponding catch per hour in Kalbak Fjord	Catch per hour in complete darkness
Sundene W of Fleserne (2)	1937	19/7	18^{35}	44–71	30	125	45	250	36	< –10	210	250
	–	3/8	22^{47}	66	30	57	13	114	23	< –10	210	114
–	–	11/8	2^{15}	72	80	401	145	301	36	< –10	210	301
–	–	11/8	4^{00}	63	30	272	82	544	30	< –10	210	544
–	–	20/8	5^{15}	61	30	177	55.5	354	31	< –10	210	354
–	–	23/8	4^{25}	69	30	190	50	380	26	< –10	210	380
–	–	23/8	5^{15}	65	30	113	43	225	38	< –10	210	225
–	–	23/8	6^{05}	70	30	112	51	224	46	–8.8	208	226
–	–	*mean*			*(290)*	*299*	*100*	*299*				*299*
–	1939	10/7	11^{00}	75	60	217	196	217	90	2.9	108	422
–	–	11/7	13^{05}	75	15	72	70	288	97	7.0	59	1025
–	–	15/7	9^{30}	76	20	118	112	355	95	5.6	72	1035
–	–	15/7	12^{10}	75	20	14	12	41	86	1.0	136	63
–	–	15/7	13^{00}	76	25	118	106	282	90	3.0	106	560
–	–	17/7	10^{15}	81	30	35	31	71	89	2.4	116	128
–	–	27/7	10^{00}	65	75	379	293	303	77	–1.0	159	400
–	–	7/8	12^{35}	77	60	106	95	106	90	3.0	106	210
–	–	7/8	14^{00}	75	60	177	160	177	90	3.0	106	350
–	–	7/8	16^{35}	76	60	180	160	180	89	2.4	116	326
–	–	11/8	9^{35}	75	60	168	150	168	89	2.4	116	304
–	–	11/8	10^{55}	73	60	205	200	205	98	8.7	48	895
–	–	11/8	13^{20}	72	60	185	175	185	95	5.6	72	540
–	–	14/8	16^{25}	74	30	140	130	280	93	4.3	87	675
–	–	14/8	17^{25}	76	30	215	200	430	98	8.7	48	1880
–	–	17/8	13^{35}	75	30	106	100	212	94	5.1	78	571
–	–	17/8	14^{35}	73	30	131	125	262	95	5.6	72	764
–	–	19/8	16^{05}	74	60	270	240	270	89	2.4	116	489
–	–	25/8	17^{00}	76	60	320	280	320	88	2.0	121	555
–	–	*mean*			*(845)*	*224*	*201*	*229*				*589*
Sundene N of the Stream (3)	1937	6/8	16^{50}	54	30	83	75	166	90	2.9	108	322
	–	6/8	18^{25}	34	20	27	27	81	100	17.0	21	810
–	–	6/8	19^{40}	60	30	55	24	110	44	–9.2	209	111
–	–	12/8	11^{00}	61	30	38	23	75	61	–5.7	194	81
–	–	12/8	11^{40}	62	30	37	25	74	68	–4.0	184	85
–	–	20/8	17^{05}	60	30	106	51	212	48	–8.3	207	215
–	–	20/8	18^{00}	60	30	211	137	422	65	–4.8	190	467
–	–	*mean*			*(200)*	*167*	*109*	*163*				*298*
Kalbak Fjord, inner part (4)	1937	22/7	14^{20}	30–45	15	20	18	79	90	3.0	106	157
	1939	9/7	9^{00}	36	60	3.5	3.2	3.5	91	3.4	100	7
–	–	11/7	9^{10}	30	30	0.3	0.3	0.6	100	17.0	21	6
–	–	12/8	17^{20}	34	30	8	8	16	100	17.0	21	160
–	–	12/8	18^{20}	52	30	17.5	17	35	97	7.0	58	127
–		25/8	15^{25}	30	30	9	9	18	100	17.0	21	180
–	–	28/8	14^{00}	28	20	11	11	33	100	17.0	21	330
–	1937–39	*mean*			*(215)*	*19*	*19*	*26*				*138*

Table 1 (continued).

Locality	Year	Date	Hour	Depth (m)	Duration of hauls (minutes)	Catch (kg) Total	Catch (kg) Large (≥ 16 cm)	Catch per hour (total)	Weight percentage of large prawns (≥ 16 cm)	Light index	Corresponding catch per hour in Kalbak Fjord	Catch per hour in complete darkness
Skaale Fjord (5)	1937	$^{20}/_{7}$	16^{50}	25	5	0.2	0.2	2.4	100	17.0	21	24
–	–	$^{20}/_{7}$	17^{45}	38	15	4.4	3.9	17.7	88	2.0	121	31
–	–	$^{24}/_{7}$	15^{50}	57	30	0.8	0.8	1.6	100	17.0	21	16
–	–	$^{24}/_{7}$	17^{03}	53	30	1	1	2	100	17.0	21	20
–	–	$^{27}/_{7}$	13^{55}	72	10	0.2	0.2	1.2	100	17.0	21	12
–	–	$^{3}/_{8}$	2^{30}	57	30	41	14	82	35	< –10	210	82
–	–	$^{20}/_{8}$	6^{40}	53	30	6.5	?	13				
–	–	*mean*			*(150)*	*22*	*10*	*17*				*31*
Kolle Fjord (6)	–	$^{19}/_{7}$	16^{45}	35	10	6	6	37	95	5.6	72	108
Arne Fjord, inner part (7)	–	$^{23}/_{7}$	16^{25}	33–53	15	6	6	25	96	6.0	66	80
Arne Fjord, outer part (8)	–	$^{23}/_{7}$	17^{20}	53	30	3	3	6	100	17.0	21	60
Bordøvig (9)	–	$^{23}/_{7}$	19^{40}	42	30	2	2	4	100	17.0	21	40
Funding Fjord, middle part (10)	–	$^{30}/_{7}$	19^{55}	33	20	1.4	1.4	4.2	100	17.0	21	42
–	–	$^{12}/_{8}$	14^{15}	48	30	1.4	1.3	2.7	93	4.3	87	7
Funding Fjord, outer part (11)	–	$^{31}/_{7}$	15^{00}	55–80	30*	0.2	0.2	0.4	100	17.0	21	4
Harald Sound, deep northern part (12)	–	$^{31}/_{7}$	17^{45}	35–88	30	2	2	4	100	17.0	21	40
Sørvaag Fjord, outer part (13)	–	$^{4}/_{8}$	20^{25}	36	30	4	4	8	100	17.0	21	80
Sørvaag Fjord, including Selvig (14)	–	$^{4}/_{8}$	21^{20}	33	30	13	13	26	100	17.0	21	260
Sundene N of whaling station (15)	–	$^{26}/_{7}$	11^{47}	24–37	20	1.6	1.3	5	80	–1.0	159	7
Kvanne Sound (16)	–	$^{25}/_{8}$	22^{35}	83	30	39	13	78	33	< –10	210	78

* a "Shrimp Trawl" with smaller meshes was used for this haul.

the hauls ended in obstacles, which lower the catch, and part of the hauls may have gone over sandy and/or rocky bottom with no *Nephrops* with the result that the catch per hour was smaller than that corresponding to the actual density on the inhabited muddy bottom. Therefore the calculated densities should be considered as minimum values.

ESTIMATION OF THE POPULATION BY MARKING

In three localities in 1937 a number of individuals were marked and liberated and after a time necessary for the marked animals to spread in the population the areas were fished again and the number and size of the recaptured marked animals noted. In two of the three places the experiment was repeated in 1939.

In 1937 the animals were marked by the extreme tip of the telson or of the exopodite of one of the uropods being cut away, a distinct mark being used for each locality.

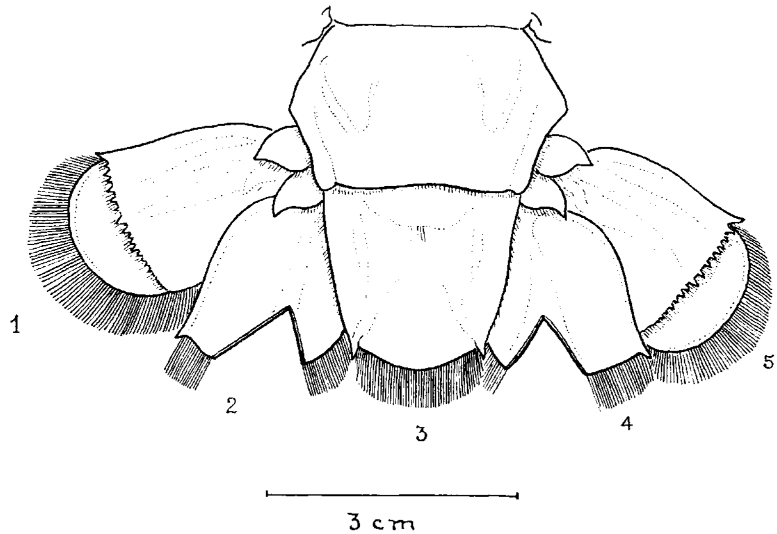

Fig. 3. "Swimming fan" of a marked specimen which has not moulted after it was marked. Being cut in the endopodites of the left and right uropods (marked: 2,4) the mark shows that the specimen was 19 cm (total length) and was marked in Kalbak Fjord 12.–14. July 1939. It was recaptured in Kalbak Fjord 26. August 1939.

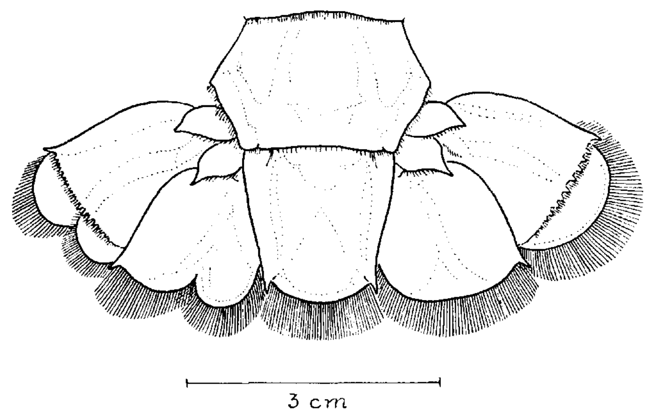

Fig. 4. "Swimming fan" of a marked specimen which has moulted after it was marked and partly regenerated the cuts. Being cut in the exopodite and endopodite of the left uropod (marked: 1,2) the mark shows that the specimen was marked in Kalbak Fjord 7.–12. May 1938 and that it was then 15 cm (total length). It was recaptured in Kalbak Fjord 20. August 1939 being 16 cm long.

In 1939 marking was done by angular cuts in one or more of the five parts of the "swimming fan" (telson, and exopodite and endopodite of the left and right uropod. While the marks in 1937 may be compared with geometric segments, the marks in 1939 resemble geometric sectors; cf. Figs. 3 and 4). By this method it was possible to mark the animals according to size.

By means of the percentage recapture the size of the populations was calculated as well as the size of their habitats. The calculations are shown in the Tables 2–8.

Table 2. Estimation of the population in Kalbak Fjord 1937.
1496 *Nephrops* from 7 hauls were marked from $^{26}/_{7}$ to $^{2}/_{8}$, but 17 were recaptured during the latter hauls for marking. Thus by $^{2}/_{8}$ 1479 marked *Nephrops* were free. The following hauls were taken for recapture:

Date	Length of haul (minutes)	Catch (kg)		Number recaptured
		Large (≥ 16 cm)	Total	
$^{9}/_{8}$	15	10	17	3
$^{9}/_{8}$	40	43	125.5	9
$^{9}/_{8}$	50	69	154	13
$^{9}/_{8}$	50	54	99	2
$^{20}/_{8}$	30	37	79.5	3
Total (5 hauls)	185	213	475	30
Recaptured percentage (by number)				2.3 %
Estimation of the population, tons		9.25	20.6	
Estimation of size of habitat, trawling hours		134		

The size of the populations is given in tons, and in addition to that of the total population the weight is given of the part of the population consisting of large animals (≥ 16 cm). The size of the habitats is measured by the number of trawling hours necessary to catch the whole population, provided the catch per hour remains constant.

In 1937 (Tables 2–4) the animals were marked irrespective of their size. Therefore, the size of the populations (total and large) and their habitats had to be calculated from one percentage of recapture, viz. that for the total population.

In 1939 (Tables 5–8) the animals were marked according to size groups of one cm, the smallest size marked being 14 cm and the upper group containing all animals larger than or equal to 20 cm (cf. Tables 5 and 7). The population of

Table 3. Estimation of the population in Sundene W of Fleserne 1937.
1838 *Nephrops* from 5 hauls were marked from $^{24}/_{7}$ to $^{4}/_{8}$, but 2 were recaptured during one of the latter hauls for marking. Thus by $^{4}/_{8}$ 1836 marked *Nephrops* were free. The following hauls were taken for recapture:

Date	Length of haul (minutes)	Catch (kg)		Number recaptured
		Large (≥ 16 cm)	Total	
$^{11}/_{8}$	80	145	401	0
$^{11}/_{8}$	30	82	272	3
$^{20}/_{8}$	30	55.5	177	3
$^{23}/_{8}$	30	50	190	2
$^{23}/_{8}$	30	42.5	112.5	3
$^{23}/_{8}$	30	51	112	2
Total (6 hauls)	230	426	1265	13
Recaptured percentage (by number)				0.71 %
Estimation of the population, tons		60	178	
Estimation of size of habitat, trawling hours		540		

Table 4. Estimation of the population in Sundene N. of the Stream 1937.
500 *Nephrops* from one haul were marked on $^{6}/_{8}$, and the following hauls were taken for recapture:

Date	Length of haul (minutes)	Catch (kg)		Number recaptured
		Large (> 16 cm)	Total	
$^{12}/_{8}$	30	23	38	1
$^{12}/_{8}$	30	25	37	1
$^{20}/_{8}$	30	51	106	0
$^{20}/_{8}$	30	137	211	3
Total (4 hauls)	120	236	392	5
Recaptured percentage (by number)				1.0 %
Estimation of the population, tons		23.6	39.2	
Estimation of size of habitat, trawling hours ..		200		

large and under-sized prawns were therefore calculated from the percentage recaptured of each category. Comparing the two years 1937 and 1939 an increase is noted in the estimated population of large prawns both in Kalbak Fjord and in Sundene W. of Fleserne. Therefore, it cannot be excluded that the size composition of the populations has really changed in the direction of more large prawns (incidentally in Sundene the fishing was not carried out in the same place in the two years; cf. p. 267). Also the size of the habitat (the number of trawling hours necessary to catch the whole population) was estimated from the percentage of recapture of each category. It will be noted that the habitat of large prawns is in both cases smaller than that of the total population. This is hardly real, as the opposite must be expected: no doubt, the larger *Nephrops* are able to live on a more sandy bottom than are the smaller ones, which must be expected to be confined to the purely muddy bottom. No doubt, the difference is due to the fact that the smaller animals are more sensitive to light (see p. 319) and are therefore exposed to be recaptured in a smaller part of the day and night than are the larger animals. Therefore, the percentage recapture of the latter is higher and the number of trawling hours correspondingly lower.

Table 5. Calculation of recaptured percentage by weight. Kalbak Fjord 1939.

Length (cm)	Calculated mean weight (g)	Marked and released		Recaptured		Recaptured percentage by weight
		number	g	number	g	
≥ 20	272	155	42160	3	816	..
19	170	103	17510	6	1020	..
18	140	123	17220	3	420	..
17	110	208	22880	9	990	..
16	90	282	25380	8	720	..
15	74	299	22126	5	370	..
14	60	280	16800	7	420	..
Large (≥ 16 cm)	..	..	125150	..	3966	3.2 %
Under-sized.....	..	..	38926	..	790	2.0 %
Total	..	..	164076	..	4756	2.9 %

Table 6. Estimation of the population in Kalbak Fjord 1939.
871 large + 579 under-sized = 1450 *Nephrops* from 5 hauls were marked from $^{12}/_{7}$ to $^{14}/_{7}$, and the following hauls were taken for recapture:

Date	Length of haul (minutes)	Catch (kg)			Number recaptured		
		Large (≥ 16 cm)	Under-sized	Total	Large (≥ 16 cm)	Under-sized	Total
$^{5}/_{8}$	35	108	47	155	5	2	7
$^{5}/_{8}$	35	50	10	60	3	2	5
$^{5}/_{8}$	35	35	5	40	1	0	1
$^{12}/_{8}$	30	17	0.5	17	1	0	1
$^{12}/_{8}$	60	80	10	90	3	0	3
$^{12}/_{8}$	60	50	40	90	1	2	3
$^{19}/_{8}$	60	80	5	85	6	0	6
$^{19-20}/_{8}$ (2 hauls).	120	90	65	155	2	3	5
$^{20}/_{8}$	60	30	2	32	0	0	0
$^{26}/_{8}$	60	100	10	110	5	3	8
$^{26}/_{8}$	70	90	60	150	2	0	2
Total (12 hauls)	625	730	254	984	29	12	41
Recaptured percentage (by number)					3.3 %	2.1 %	2.8 %
Estimation of the population, tons..................		22.1	12.1	35.1	..	..	..
Estimation of size of habitat, trawling hours		316	496	372	..	..	..
Recaptured percentage (by weight, cf. Table 5)..............					3.2 %	2.0 %	2.9 %
Estimation of the population, tons..................		22.6	12.7	34.0	..	..	..
Estimation of size of habitat, trawling hours		326	521	360	..	..	..

For 1939 it is possible to estimate the size of the populations also from the recaptured percentage by weight, using our knowledge of the size of the marked and recaptured prawns and the estimate of the mean weight of animals belonging to each size group (cf. p. 294). The calculation of the percentage recapture as to

Table 7. Calculation of recaptured percentage by weight. Sundene W. of Fleserne 1939.

Length (cm)	Calculated mean weight (g)	Marked and released		Recaptured		Recaptured percentage by weight
		number	g	number	g	
≥ 20	272	189	51408	5	1360	..
19	170	185	31450	6	1020	..
18	140	203	28420	6	840	..
17	110	242	26620	3	330	..
16	90	238	21420	3	270	..
15	74	168	12432	0	0	..
14	60	91	5460	0	0	..
Large (> 16 cm) ..	..	..	159318	..	3820	2.4 %
Under-sized......	..	..	17892	..	0	0.0 %
Total	..	..	177210	..	3820	2.2 %

Table 8. Estimation of the population in Sundene W. of Fleserne 1939.
1057 large + 259 under-sized = 1316 *Nephrops* from 5 hauls were marked from $^{11}/_{7}$ to $^{17}/_{7}$, and the following hauls were taken for recapture:

Date	Length of haul (minutes)	Catch (kg) Large	Catch (kg) Under-sized	Catch (kg) Total	Number recaptured Large	Number recaptured Under-sized	Number recaptured Total
$^{7}/_{8}$	60	95	11	106	2	0	2
$^{7}/_{8}$	60	160	17	177	5	0	5
$^{7}/_{8}$	60	160	20	180	2	0	2
$^{11}/_{8}$	60	150	18	168	3	0	3
$^{11}/_{8}$	60	200	5	205	0	0	0
$^{11}/_{8}$	60	175	10	185	1	0	1
$^{14}/_{8}$	30	130	10	140	1	0	1
$^{14}/_{8}$	30	200	15	215	0	0	0
$^{17}/_{8}$	30	100	6	106	2	0	2
$^{17}/_{8}$	30	125	6	131	0	0	0
$^{19}/_{8}$	60	240	30	270	2	0	2
$^{25}/_{8}$	60	280	40	320	5	0	5
Total (12 hauls)	600	2015	188	2203	23	0	23
Recaptured percentage (by number)					2.2 %	0 %	1.7 %
Estimation of the population, tons..................		91.5	–	130	..	..	..
Estimation of size of habitat, trawling hours		455	–	590	..	..	..
Recaptured percentage (by weight, cf. table 7)..............					2.4 %	0 %	2.2 %
Estimation of the population, tons..................		84		100	..	..	..
Estimation of size of habitat, trawling hours		416	–	455	..	..	..

weight is shown in the Tables 5 and 7, and the sizes of the populations and their habitats estimated by means of the weights are given at the bottom of the Tables 6 and 8. It will be noted that the order of magnitude of the estimates is the same whether based on numbers or weights.

The result of the marking experiments may be checked against the catch per hour found by fishing. This is shown in Table 9: The total population of large

Table 9. Comparison of the catch per hour estimated by marking experiments and that found by fishing.

Locality	Sundene N. of the Stream	Kalbak Fjord	Sundene W. of Fleserne	Kalbak Fjord	Sundene W. of Fleserne
Year	1937	1937	1937	1939	1939
Total population of large prawns (t)	23.6	9.25	60	22.3	88
Habitat (trawling hours)	200	134	540	320	435
Large, kg/hour (= 40 % of total)..	118	69	111	69.5	202
Total catch/hour (kg)					
Estimated by marking	296	172	278	173	505
Estimated by fishing (from Table 1)	298	210	299	210	589

Nephrops is divided by the size of the habitat (in trawling hours) to give the catch of large *Nephrops* (≥ 16 cm) in kg per hour. According to Fig. 22 this equals 40 % of the total population (next row), which may be compared with the catch per hour found by fishing and corrected for the influence of the light (from Table 1). The density of the population found by marking should be compared with that found by fishing in total darkness, because marked animals have the same probability as other individuals of being caught, irrespective of the intensity of the light. The calculations are based on the population of large *Nephrops* found by marking, because very few under-sized individuals were marked, so the estimation of the under-sized part of the population is not very reliable. The last two rows in Table 9 show a good agreement between the density of the population found by marking and by fishing. It might be pointed out that both figures are functions of the catch per hour found by fishing, but it should be remembered the figures taken from Table 1 (the bottom row in Table 9) have been corrected for the effect of the light, so Table 9 gives a check of the consistency of all these calculations.

MORPHOLOGY

JUVENILE STAGES

Collecting the material

The larval stages were collected with a stramin net. The data of the catches of these stages are shown in Table 10.

The postlarvae and the smallest adults were collected in the following way:

1) 22 postlarvae, 1 ♀ of 38 mm, and 1 ♀ of 42 mm from stomachs of *Raja clavata* of about 50 cm length caught in the inner part of Kalbak Fjord 12. VIII. 1939, 18^{20} hours. Depth: 50 m; bottom material: mud.

2) 11 postlarvae, 1 ♂ of 35 mm, and 1 ♀ of 42 mm from stomachs of *Raja clavata* of about 50 cm length caught in the outer part of Kalbak Fjord 12. VIII. 1939, 20^{00} hours. Depth: 50 m; bottom material: mud.

3) 3 postlarvae and 1 ♂ of 48 mm from Kalbak Fjord 14. VIII. 1939, 24^{00} hours. Depth: 50 m. Bottom material (mud) was taken by a fish basket tied to one end of one trawl wire. The mud was washed through 3 sieves.

From the list of the material (Table 10) it is obvious that no special difficulties were encountered in collecting the first and second larval stages, two hauls with a 200 cm stramin net giving 2340 specimens of the first and 280 of the second stage. Of the third stage, however, a total of only 6 specimens were known after the investigations in Faeroe waters and of the postlarvae only 4 specimens were known from the literature before these investigations. As according to its morphology the third larval stage must be considered pelagic as well as the first and second stage, it is reasonable to believe that a copious material of the third stage would be secured by hauls with a stramin net on a somewhat later date (the end of May or the beginning of June).

It is otherwise with the postlarvae. This stage is living in and on the bottom, and owing to its small size and its ability to swim fast it has to be caught by a big, small mesh, rather fast moving gear, and all known gear with these characteristics will invariably be lost in the soft bottom in which the species lives. Therefore, it

Table 10. Catches of *Nephrops* larvae with stramin net in Faeroe waters 1927–1939.

Date	Year	Hour	Locality	Diameter of net (cm)	Length of wire (m)	Approximate initial depth (m)	Duration of haul (min.)	Larvae number	Larvae stage
30/4	1934	8^{50}	Sundene W. of of Fleserne	200	65	..	15	14	1.
30/4	1934	10^{10}	Kalbak Fjord	200	65	..	15	3	1.
4/5	1934	6^{05}	Arne Fjord	200	65	..	15	ca. 80 22	1. 2.
11/5	1938	8^{10}	Sundene W. of Fleserne	200	100 reduced step-wise	..	30	1190 100 1	1. 2. 3.
11/5	1938	16^{55}	Kalbak Fjord	200	100 reduced step-wise	..	30	1152 178 1	1. 2. 3.
28/6	1927	8^{45}	Kalbak Fjord	200	20	..	30	a few not identified	
28/6	1927	9^{40}	Kalbak Fjord	200	20	..	30	a few not identified	
28/6	1927	11^{10}	Sundene W. of Fleserne	200	65	..	15	a few not identified	
26/7	1933	18^{05}	Sundene W. of Fleserne	200	65	..	15	few	? 1.
26/7	1933	18^{50}	Skaale Fjord	200	65	..	15	few	? 1.
27/7	1939	15^{00}	Skaale Fjord	150	..	50	vertical	1 1	1. 2.
21/8	1939	13^{50}	Kolle Fjord	150	..	38	vertical	1	1.
23/8	1937	8^{00}	Sundene W. of Fleserne	200	..	47	vertical	1	1.
23/8	1937	9^{40}	Kalbak Fjord	200	..	59	vertical	1	1.
23/8	1937	11^{15}	Skaale Fjord	200	..	54	vertical	7	1.
23/8	1937	11^{45}	Skaale Fjord	200	..	50	vertical	5	1.
23/8	1937	12^{45}	Sundene W. of Fleserne	200	..	45	vertical	1	1.
23/8	1927	16^{50}	Funding Fjord	200	35	..	15	a few not identified	

will be difficult to secure a representative material of the postlarva. As a matter of fact the rather big number of this stage from the Faeroes was not taken directly with a fishing gear, but was found in the stomachs of *Raja clavata*, and accordingly these specimens were somewhat damaged by digestion. The only three living post-larvae known from the Faeroes were taken with a very unusual gear, viz. a fish basket fixed to the end of one trawl wire and hauled for a short distance over the bottom. (It is possible that an extremely small mesh attachment inside or outside the cod-end would be able to catch this smallest bottom stage of *Nephrops*. Sars (1884, p. 164) got his specimen in a dredge).

A comparison shows good agreement in all essential features between *Nephrops* larvae from the Faeroes and the descriptions and drawings by Sars (1884 and 1889), Jørgensen (1925), and Santucci (1926 and 1927). It should be mentioned, however, that the exopodites of the third pair of maxillipeds and of the pereiopods

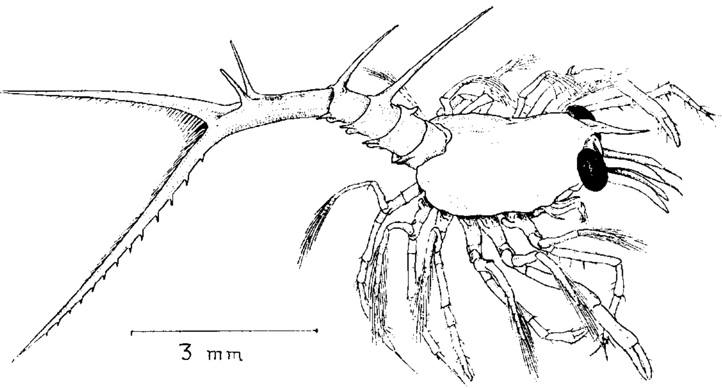

Fig. 5. The first larval stage (*Zoëa*), total length: 7 mm.

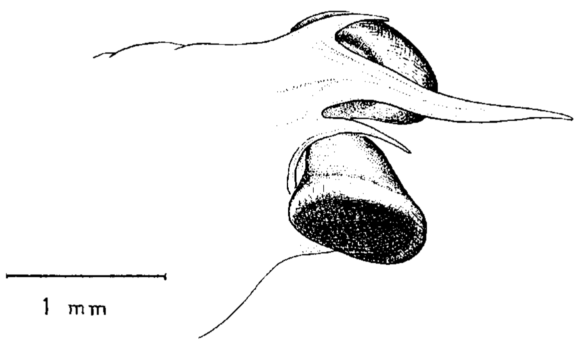

Fig. 6. Anterior part of the second larval stage (first *Mysis* stage, total length: 9 mm) showing the rostrum and the spines above the eyes.

are attached to the second segment of these legs (basis), as usual in crustaceans, and not, as stated by Santucci (1926, p. 23), to their third segment (ischium). Santucci shows this himself quite clearly in several figs. (1927, Figs. 16, 17, and 20), and also the rudimentary exopodites in Fig. 1 (loc. cit.) are correctly drawn, while all his outline drawings of the larvae show the exopodites erroneously attached to the third segment.

The first larval stage (*Zoëa*) is shown in Fig. 5. There is nothing essential to add to the earlier descriptions of this stage. Details of the second larval stage (first *Mysis* stage) are shown in Figs. 6 and 7. Santucci (1926, Plate 2, Fig. 2) shows preformation of the uropods; this is more clearly seen in a Faeroe specimen (Fig. 7), which has obviously been about to moult. It will be noted that the uropods are preformed with their distal end pointing forward. The third larval stage (second *Mysis* stage, Fig. 8) has the telson immovably fixed to the preceeding segment. There is no articulation between them as stated by Sars.

A postlarva is shown in Fig. 9. All examined specimens from the Faeroes (15–23 mm) had rudiments of exopodites on the pereiopods. These rudiments were

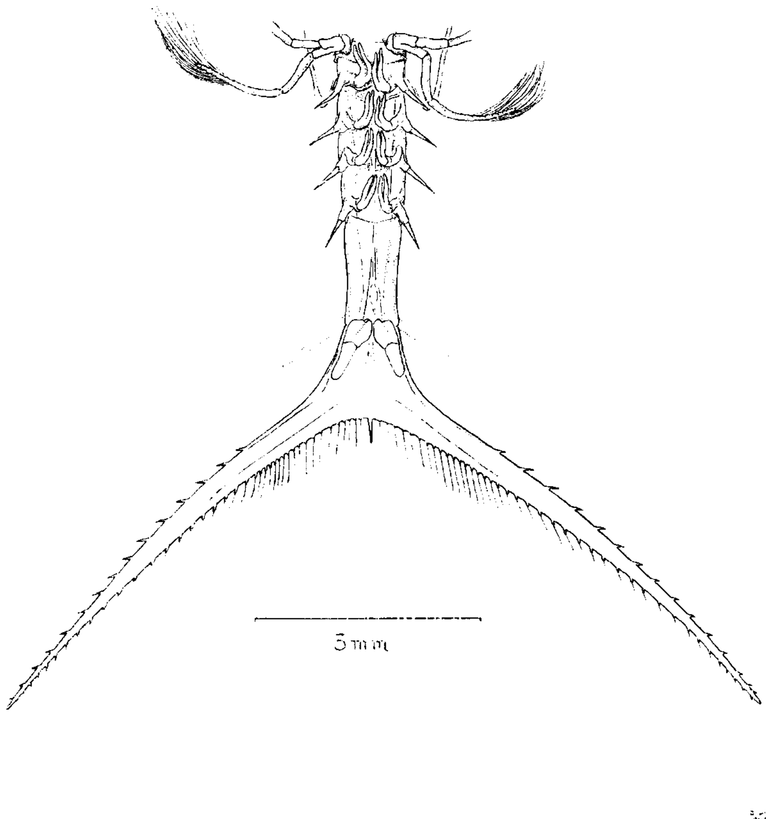

Fig. 7. Abdomen of the second larval stage (same specimen as Fig. 6) showing pleopods and preformation of uropods.

invariably situated at the distal end of the basis, as drawn by Santucci (1927, Fig. 1). Their size varied as a rule inversely with the size of the animal. Therefore it is not likely that the two post larvae described and drawn by Santucci represent distinct stages, but rather that the postlarval stage represents several instars with successive reduction of the rudiments of the exopodites.

In all postlarvae from the Faeroes the oral (lateral) branch of the uropods had two segments as in the adult *Nephrops*.

Table 11 shows the distribution according to size of all measured larvae and postlarvae from Faeroe waters, and Table 12 gives the length of juvenile stages known before this investigation.

Table 11.

Distribution according to total length of juvenile stages of *Nephrops* from Faeroe waters. All larvae are from Sundene 1938, except 1 *Zoëa* of 5 mm and 1 *Mysis* II from Kalbak Fjord 1938. The postlarvae are all from Kalbak Fjord 1939.

Stage	*Zoëa*	*Mysis* I	*Mysis* II	Postlarva	*Nephrops*	Length in mm
Date	$^{11}/_{5}$	$^{11}/_{5}$	$^{11}/_{5}$	$^{12\text{-}14}/_{8}$	$^{12\text{-}14}/_{8}$	
Length in mm						
48	..	..	..	..	1 ♂	48
47	..	..	..	..	..	47
46	..	..	..	..	..	46
45	..	..	..	..	..	45
44	..	..	..	..	..	44
43	..	.	..	..	..	43
42	..	..	..	..	2 ♀	42
41	..	..	..	..	..	41
40	..	..	..	..	..	40
39	..	..	..	..	..	39
38	..	..	..	..	1 ♀	38
37	..	..	..	..	..	37
36	..	..	..	..	..	36
35	..	..	..	..	1 ♂	35
34	..	..	..	..	..	34
33	..	..	..	..	..	33
32	..	..	..	..	..	32
31	..	..	..	..	..	31
30	..	..	..	..	..	30
29	..	..	..	..	..	29
28	..	..	..	..	..	28
27	..	..	..	..	..	27
26	..	..	..	..	..	26
25	..	..	..	..	..	25
24	..	..	..	..	..	24
23	..	..	..	1	..	23
22	..	..	..	1	..	22
21	..	..	..	1	..	21
20	..	..	..	2	..	20
19	..	..	..	..	..	19
18	..	..	..	6	..	18
17	..	..	..	12	..	17
16	..	..	..	7	..	16
15	..	..	..	3	..	15
14	..	..	..	..	..	14
13	..	..	..	..	..	13
12	..	..	..	..	..	12
11	..	..	2	..	..	11
10	..	..	..	..	..	10
9	..	12	..	..	..	9
8	..	19	..	..	..	8
7	26	3	..	..	..	7
6	24	1	..	..	..	6
5	1	..	..	..	..	5

Table 12. Distribution according to total length of juvenile stages known before the investigations in Faeroe waters.

S. = Sars (1884 and 1889), J. = Jørgensen (1925), and Sant. = Santucci (1926 and 1927).

Stage........	*Zoëa*		*Mysis* I		*Mysis* II		Postlarva		Length in mm
Authors ..... Length in mm	J.	Sant.	S. + J.	Sant.	S. + J.	Sant.	S. + J.	Sant.	
17	..	..	..	..	..	..	..	1	17
16	..	..	..	..	..	..	..	..	16
15	..	..	..	..	..	..	..	1	15
14	..	..	..	..	..	..	..	..	14
13	..	..	..	..	..	..	..	..	13
12	..	..	..	..	..	1	1	..	12
11	..	..	..	..	..	1	1	..	11
10	..	..	..	..	2	..	..	..	10
9	..	..	..	..	..	..	..	..	9
8	..	..	1	4	..	..	..	..	8
7	..	2	1	1	..	..	..	..	7
6	1	6	..	..	..	..	..	..	6
5	..	1	..	..	..	..	..	..	5

ADULTS

Size

Overall length of the adults.

As the *Nephrops* is growing during the whole of its life a complete description of its size at a given locality would require the frequency distribution according to size of all individuals in a representative sample of the population, and this would be equal to a graph of the survival according to size. However, a representative sample cannot be secured, because the composition of a catch is a function of the intensity of the light as well as the gear used.

For the same reason the average sizes of the two sexes in a sample have only a very slight relation to any property of the population, and two populations cannot be compared by means of these averages even if the same gear has been used for the investigation of both of them.

However, the maximum sizes reached by males and females in the catches are independent of the mesh size and the intensity of the light and may therefore serve for a comparison of the size of the *Nephrops* at various localities. Table 13 shows that the Faeroe *Nephrops* does not differ conclusively in size from other populations, not even from those of the Adriatic. (It can not be excluded that the males in Faeroe waters may be bigger than those in the Adriatic).

Another figure which might characterize different populations is the size at which maturity is reached. This has rarely been investigated in males (Storrow (1913, p. 16) records 10 cm as the length of the smallest mature male), but the smallest berried female is often recorded. Table 14 gives the records of the smallest berried female from a number of localitites. There is a considerable variation, but it is hardly due to any property of the populations, as it is well correlated with the smallest individual caught, which shows that it is a function of the mesh size: in the Clyde area a small mesh attachment was used (Thomas 1954, p. 3) and the

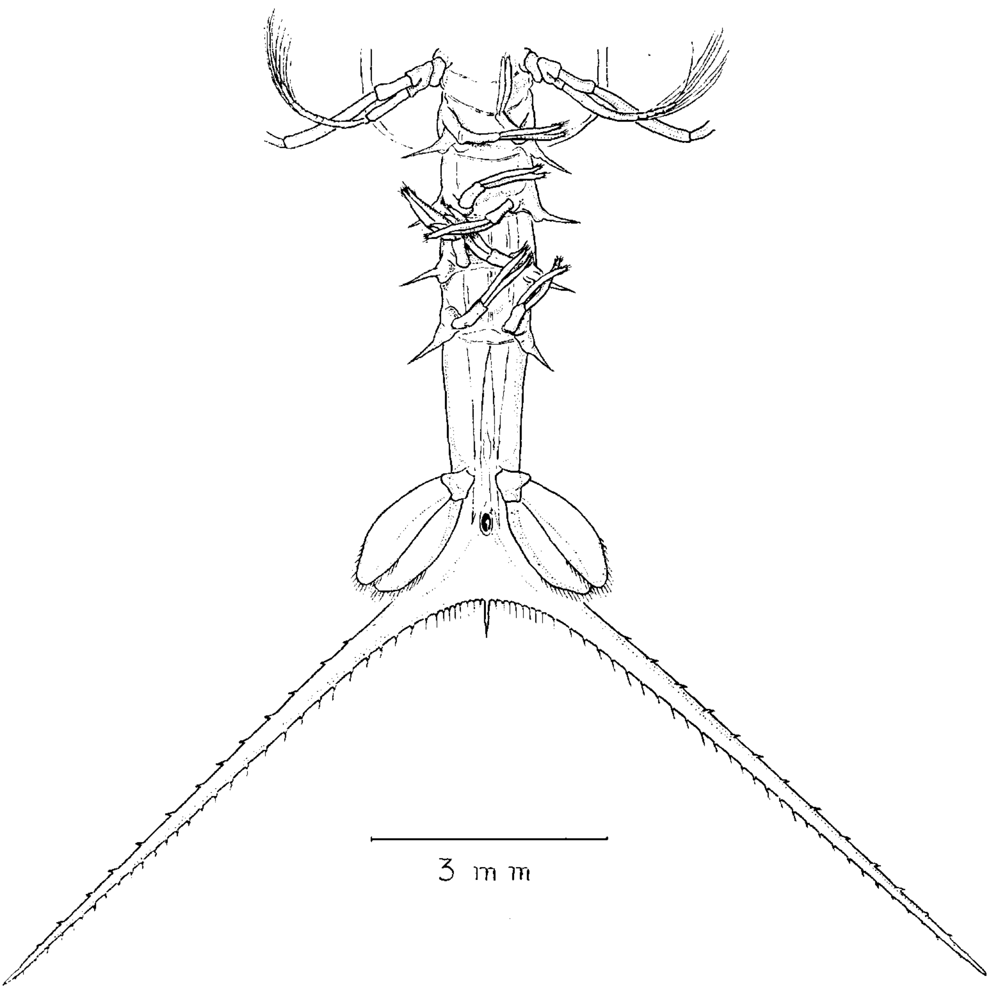

Fig. 8. Abdomen of the third larval stage (second *Mysis* stage, total length: 11 mm, from Sundene W. of Fleserne. 11. May 1938) showing pleopods and uropods.

trawl used in the Adriatic had very small meshes (26 mm) in the cod-end (Karlovac 1953, p. 4).

For this reason a population is better characterized by the average size at which the females start spawning and this average may be estimated from the graphs of the sex ratio plotted against the size. Table 15 shows these estimates from the localities for which representative graphs of the sex ratio can be drawn (cf. p. 312). The table shows that the figure for Faeroe waters do not differ from those from the Adriatic, but that for North Shields is higher. It must be remembered,

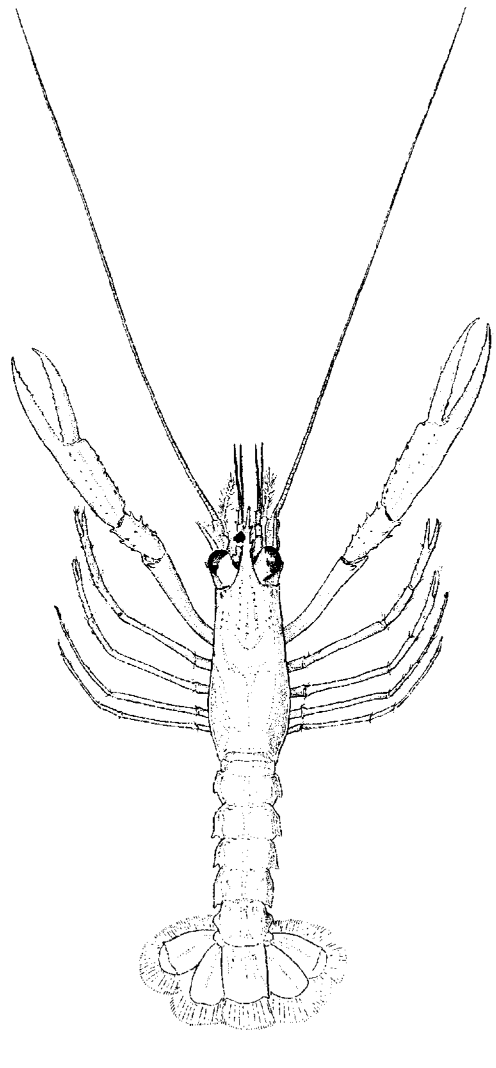

Fig. 9. Postlarva (total length: 16 mm, from Kalbak Fjord 14. August 1939).

however, that these figures may be influenced by the distribution of the samples throughout the year, especially if various size groups of females do not spawn at the same time.

Length of the carapace.

For the description of the adult *Nephrops* some measurements of the length of the carapace are of interest. The 20. August 1937 the length of the carapace as well as the total length was measured of 285 living individuals (194 males and 91 females) caught in Sundene North of the Stream. The length of the carapace

Table 13. Length (from the point of the rostrum to the end of the telson) of the largest individual of each sex caught at various localities. The figures give the lower limit of the one-cm size group.

Locality	Length (cm) of largest	
	Male	Female
Kalbak Fjord	23	16
Sundene West of Fleserne	23	15
Other Faeroe localities	26	19
North Shields (Storrow 1912)	21.5	16.5
Scottish waters (McIntosh 1909)	21.5	16.5
Firth of Clyde (Thomas 1954)	24	18
Clyde area (Barnes & Bagenal 1951)	23	14
Skagerrak and Kattegat (Höglund 1942)	24	19
Skagerrak and Kattegat (Poulsen 1946)	25	20
North Adriatic channel region (Karlovac 1953)	20	17
High Adriatic (Karlovac 1953)	22	19

Table 14. Length of smallest berried female recorded at various localities. The figures give the lower limit of the one-cm size groups.

Locality	Length (cm) of smallest	
	berried female	individual caught
Faeroe waters	9	5
North Shields (Storrow 1912, p. 17)	7.5	4.5
Clyde area (Bagenal 1953, p. 212)	7	?
Firth of Clyde (Thomas 1954, p. 7)	7	3
Skagerrak and Kattegat (Höglund 1942, p. 295)	about 10	?
Skagerrak and Kattegat (Poulsen 1946, p. 34)	10	8
North Adriatic channel region (Karlovac 1953, p. 12)	8	4
High Adriatic (Karlovac 1953, p. 11)	6	3

Table 15. Average size at which the females get berried as estimated from the graphs of the sex ratio plotted against the size. The table shows the abcissa of the first point showing a significant increase in the female sex ratio above 50 %. (The figures give the lower limit of the one-cm size group).

Locality	Average size at maturation (cm)
Faeroes	8–9
North Shields (Storrow 1912)	10.5
North Adriatic channel region (Karlovac 1953)	9
High Adriatic (Karlovac 1953)	8

Table 16. Two-dimentional distribution of 194 male *Nephrops* according to length of carapace (mm) and total length (cm). The coordinates have not been correted according to the fact that the measurements were taken to the nearest unit below. (For further details see the text).

Total (cm)	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Carapace (mm)																			
105	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
100	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
99	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
98	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
97	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
96	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
95	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
94	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
93	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..
92	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
91	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..
90	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..
89	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	1	..	..	..
88	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
87	..	..	..	..	..	..	..	..	..	..	..	..	..	1	4	..	..	..	..
86	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..
85	..	..	..	..	..	..	..	..	..	..	..	..	..	5	3	..	..	..	..
84	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..
83	..	..	..	..	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..
82	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..
81	..	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..
80	..	..	..	..	..	..	..	..	..	..	..	..	4	2	..	..	..	..	..
79	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..
78	..	..	..	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..
77	..	..	..	..	..	..	..	..	..	..	..	2	6	..	..	..	..	..	..
76	..	..	..	..	..	..	..	..	..	..	..	3	6	..	..	..	..	..	..
75	..	..	..	..	..	..	..	..	..	..	..	3	1	..	..	..	..	..	..
74	..	..	..	..	..	..	..	..	..	..	..	2	2	..	..	..	..	..	..
73	..	..	..	..	..	..	..	..	..	..	..	8	1	..	..	..	..	..	..
72	..	..	..	..	..	..	..	..	..	..	1	4	..	..	..	..	..	..	..
71	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..
70	..	..	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..
69	..	..	..	..	..	..	..	..	..	..	7	..	..	..	..	..	..	..	..
68	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
67	..	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..
66	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
65	..	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..
64	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..
63	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..
62	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
61	..	..	..	..	..	..	..	..	7	1	..	..	..	..	..	..	..	..	..

Table 16 (continued).

Total (cm)	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Carapace (mm)																			
60	..	..	..	..	..	..	..	..	6	..	..	..	..	..	..	..	..	..	..
59	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	..	..
58	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
57	..	..	..	..	..	..	..	6	1	..	..	..	..	..	..	..	..	..	..
56	..	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..
55	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
54	..	..	..	..	..	..	1	4	..	..	..	..	..	..	..	..	..	..	..
53	..	..	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..
52	..	..	..	..	..	..	5	1	..	..	..	..	..	..	..	..	..	..	..
51	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..
50	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..
49	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..
48	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..
47	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..
46	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..
45	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
44	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
43	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..
42	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
41	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
40	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
39	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
31	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

was measured to the nearest millimeter below from the tip of the rostrum to the posterior edge of the carapace, excluding the setae, and the total length as usual to the nearest centimeter below from the tip of the rostrum to the end of the telson, excluding the setae. These measurements are presented in the Tables 16 and 17. In Table 18 the mean length of the carapace corresponding to the total length in cm groups is given for males and females, together with the difference between males and females. The table shows that as a rule the females have a comparatively longer abdomen, although the difference is small and not so striking as might have been expected in view of the breeding biology; exceptions to the rule are found in the largest females, where positive as well as negative deviations are greater.

This series of measurements of living animals was supplemented by a number of measurements of small, preserved animals, which are given in the Tables 19 and 20. It may be added that the length of the carapace of one specimen of each

Table 17. Two-dimentional distribution of 91 female *Nephrops* according to length of carapace (mm) and total length (cm). The coordinates have not been corrected according to the fact that the measurements were taken to the nearest unit below.

(For further details see the text).

Total (cm)	7	8	9	10	11	12	13	14	15	16
Carapace (mm)										
77	..	..	..	..	..	..	..	..	..	1
76	..	..	..	..	..	..	..	..	..	..
75	..	..	..	..	..	..	..	..	..	1
74	..	..	..	..	..	..	..	..	..	..
73	..	..	..	..	..	..	..	..	..	..
72	..	..	..	..	..	..	..	..	..	..
71	..	..	..	..	..	..	..	..	..	..
70	..	..	..	..	..	..	..	..	2	..
69	..	..	..	..	..	..	..	..	..	..
68	..	..	..	..	..	..	..	..	2	..
67	..	..	..	..	..	..	..	2	..	..
66	..	..	..	..	..	..	..	2	1	..
65	..	..	..	..	..	..	..	..	1	..
64	..	..	..	..	..	..	..	1	..	..
63	..	..	..	..	..	..	2	2	..	..
62	..	..	..	..	..	..	..	1	..	..
61	..	..	..	..	..	..	3	..	..	..
60	..	..	..	..	..	..	4	..	..	..
59	..	..	..	..	..	..	4	..	..	..
58	..	..	..	..	..	1	4	..	..	..
57	..	..	..	..	..	4	1	..	..	..
56	..	..	..	..	..	4	..	..	..	..
55	..	..	..	..	..	5	..	..	..	..
54	..	..	..	..	1	3	..	..	..	..
53	..	..	..	..	1	2	..	..	..	..
52	..	..	..	..	2	1	..	..	..	..
51	..	..	..	..	2	1	..	..	..	..
50	..	..	..	..	3	..	..	..	..	..
49	..	..	..	..	1	..	..	..	..	..
48	..	..	..	3	1	..	..	..	..	..
47	..	..	..	2	..	..	..	..	..	..
46	..	..	..	2	..	..	..	..	..	..
45	..	..	..	3	..	..	..	..	..	..
44	..	..	3	..	..	..	..	..	..	..
43	..	..	2	..	..	..	..	..	..	..
42	..	..	1	..	..	..	..	..	..	..
41	..	..	3	..	..	..	..	..	..	..
40	..	1	1	..	..	..	..	..	..	..
39	..	2	..	..	..	..	..	..	..	..
38	..	..	..	..	..	..	..	..	..	..
37	..	1	..	..	..	..	..	..	..	..
36	1	..	..	..	..	..	..	..	..	..

Table 18. Mean length of carapace corresponding to one-cm groups of total length. The one-cm groups are named by their lower limits, and the length of the carapace has not been corrected according to the fact that it has been measured to the nearest millimeter below.

Total length (cm)	Mean length of carapace (mm)		Difference
	Males	Females	
23	105	..	..
22	..	..	..
21	97.3	..	..
20	91.5	..	..
19	86.7	..	..
18	83.2	..	..
17	77.3	..	..
16	73.6	76.0	−2.4
15	69.1	67.8	1.3
14	64.3	64.8	−0.5
13	60.1	59.7	0.4
12	55.4	55.0	0.4
11	51.5	50.9	0.6
10	47.2	46.5	0.7
9	42.8	42.3	0.5
8	39.0	38.8	0.2
7	..	36	..
6	31	..	..

Table 19. Two-dimentional distribution according to total length (cm) and length of carapace (mm) of 17 small, preserved *Nephrops* caught in Kalbak Fjord 14.–20. August 1939.

Total (cm)	Males				Females			
	4	5	6	7	5	6	7	8
Carapace (mm)								
37	..	..	..	..	..	..	..	1
36	..	..	..	..	..	..	..	..
35	..	..	..	1	..	..	1	..
34	..	..	..	..	..	..	2	..
33	..	..	..	2	..	..	3	..
32	..	..	1	1	..	..	..	..
31	..	..	1	..	..	..	..	..
30	..	..	..	..	..	1	..	..
29	..	1	..	..	..	..	..	..
28	..	..	..	..	..	..	..	..
27	..	..	..	..	..	..	..	..
26	..	..	..	..	1	..	..	..
25	..	..	..	..	..	..	..	..
24	..	..	..	..	..	..	..	..
23	..	..	..	..	..	..	..	..
22	1	..	..	..	..	..	..	..

Table 20. Total length and carapace length of 3 preserved postlarvae from Kalbak Fjord 14. August 1939.

Total length (mm)	Carapace length (mm)
22	10
17	8
16	7

of the larval stages was 3.0 mm, 4.5 mm, and 6 mm in the first, second, and third larval stage, respectively.

As was to be expected the regression line of the carapace length on the total length passes approximately through the origin. Therefore, it is reasonable to calculate the fraction of the total length taken up by the carapace, or, in other words, the mean length of the carapace in each cm-group divided by the total length. This is given in Table 21, which shows that the fraction of the body taken up by the carapace is fairly constant, but perhaps it is relatively large in small animals as both in males and females the fraction decreases steadily up to 12 cm total length. This seems to be confirmed by the figures for the small preserved animals given in Table 22. However, the figures are somewhat smaller for the postlarvae.

Measurements of the length of the carapace have already been published by Thomas (1954, Fig. 5, p. 11), but they are not comparable with those above, for they were taken from the hinder end of the eye socket, not from the tip of the

Table 21. Average carapace length divided by total length for one-cm groups of total length, calculated from the observations presented in the Tables 16 and 17 after correcting for bias of measurements by adding 0.5 units.

Total length (cm)	Average carapace length/total length	
	Males	Females
23.5	0.450	..
22.5	..	..
21.5	0.455	..
20.5	0.449	..
19.5	0.447	..
18.5	0.452	..
17.5	0.444	..
16.5	0.449	0.464
15.5	0.449	0.440
14.5	0.446	0.450
13.5	0.449	0.445
12.5	0.447	0.444
11.5	0.452	0.446
10.5	0.454	0.448
9.5	0.455	0.450
8.5	0.465	0.462
7.5	..	0.486
6.5	0.485	..

Table 22. Average carapace length divided by total length for one-cm (or one-mm) groups of total length, calculated from the observations on preserved animals presented in the Tables 19 and 20 after correcting for bias of measurements by adding 0.5 units.

Total length (cm)	Average carapace length/total length	
	Males	Females
8.5	..	0.441
7.5	0.450	0.456
6.5	0.492	0.470
5.5	0.536	0.581
4.5	0.500	..
(mm)	Postlarvae	
22.5	0.467	
17.5	0.485	
16.5	0.455	

rostrum. His regression line goes from 120 mm total at 36 mm carapace to 180 mm total at 59.4 mm carapace. Adding 0.5 mm as correction for bias of measurement and dividing, we get:

total length	carapace length/total length
180.5 mm	0.332
120.5 mm	0.303

Thus, measured in this way the fraction taken up by the carapace seems to increase with increasing size.

Length including the claws.

In 10 particularly large *Nephrops* of both sexes and one particularly small female the length including the claws was measured. The figures are given in Table 23. As was to be expected the claws are comparatively longer in the males than in the females. Such measurements would be of interest also in small individuals in order to see at what size the above sexual difference is detectable.

Weight.

Earlier investigations.

Poulsen (1946, p. 34) gives the weight of males, non-berried and berried females for each cm-group. He finds that the weight of the non-berried females is smaller, that of the berried females bigger than the weight of the males. He also finds that the males are heavier in November than in April and attributes this to a better nutritional condition in the autumn. He calculates a "nutritional coefficient" dividing the weight by the third power of the length and finds that this quotient increases with the length of the males. He attributes this partly to a better nutritional condition, partly to a relative heavier shell of the larger individuals (cf. remarks below on heavier claws).

Table 23. Length including the claws. The length (mm) from the tip of the claws to the end of the telson (excluding and including its setae) is compared with the "total length" (mm) from the tip of the rostrum to the end of the telson (excluding and including its setae). The specimens were measured at the following localities: no. 1: Harald Sound 31. July 1937, 17^{45}; no. 2: Sundene just North of the whaling station, North of Thorsvig 26. July 1937, 11^{47}; no. 3: Bordøvig 23. July 1937, 19^{10}; no. 4: Skaale Fjord 3. August 1937, 2^{30}; no. 5: Sundene North of the Stream 6. August 1937, 16^{50}–19^{10}; no. 6: Sundene West of Fleserne. 4. August 1937, 0^{50}.

		Total length		Length including claws		
Locality	Sex / Setae of telson	Excluded (a)	Included (b)	Excluded (c)	Included (d)	c/a
1	♂	259	265	474	480	1.83
1	♂	257	263	462	468	1.80
1	♂	245	251	466	472	1.90
2	♂	251	258	424	431	1.69
3	♂	241	246	439	444	1.82
3	♂	233	238	423	428	1.82
4	♀	173	178	256	261	1.48
5	♀	187	192	286	291	1.53
5	♀	178	183	267	272	1.50
5	♀	163	168	251	256	1.54
6	♀	66	70	92	96	1.39

Investigations at the Faeroes.

In Faeroe waters in 1937 and 1939 altogether 1370 *Nephrops* were weighed by a kitchen balance with a movable weight, the smallest unit being 2 g and the highest load 5 kg. Unfortunately (and unlike the measuring) the weighing was not made to the nearest unit (even gram) below, but to the nearest gram. In most samples this has resulted in all frequencies of even grams being higher than the neighboring ones of odd grams, in some fewer cases it is the odd that are most frequent. However, there is no tendency of the frequencies to pile up (or avoid) multiplies of 10, so if the frequencies of all odd groups are added to the nearest even ones below the resulting distributions seem rather reliable.

The mean weights for each cm-group are given in Table 24 for males and non-berried, berried, and soft-shelled females. It will be noticed that the males are heavier than the non-berried females. This difference was also found by Poulsen (1946) in the Danish population and is no doubt due to heavier claws of the males. The weight of berried females is about that of the males and does not exceed it as obviously as in the Danish population, but observations are few so this difference remains to be confirmed by future investigations. As was to be expected the soft-shelled females are lighter than the hard-shelled ones.

Compared with the Danish *Nephrops* of the same length the Faeroe animals are the heavier, and this applies equally to males, non-berried and berried females. The cause of this difference is not clear. It is not due to the fact that the Danish observations include many light animals from April, because it is also the case with animals of 20 cm or more and here the observations from November are in the majority in the Danish observations.

If the logarithm of the mean weight is plotted against the logarithm of the length (Fig. 10) two straight lines are formed for the males, one below and one above the 15 cm-group (15.5). As most of the females are below 15 cm this means that when the males exceed the size of the ordinary female the allometry changes; most

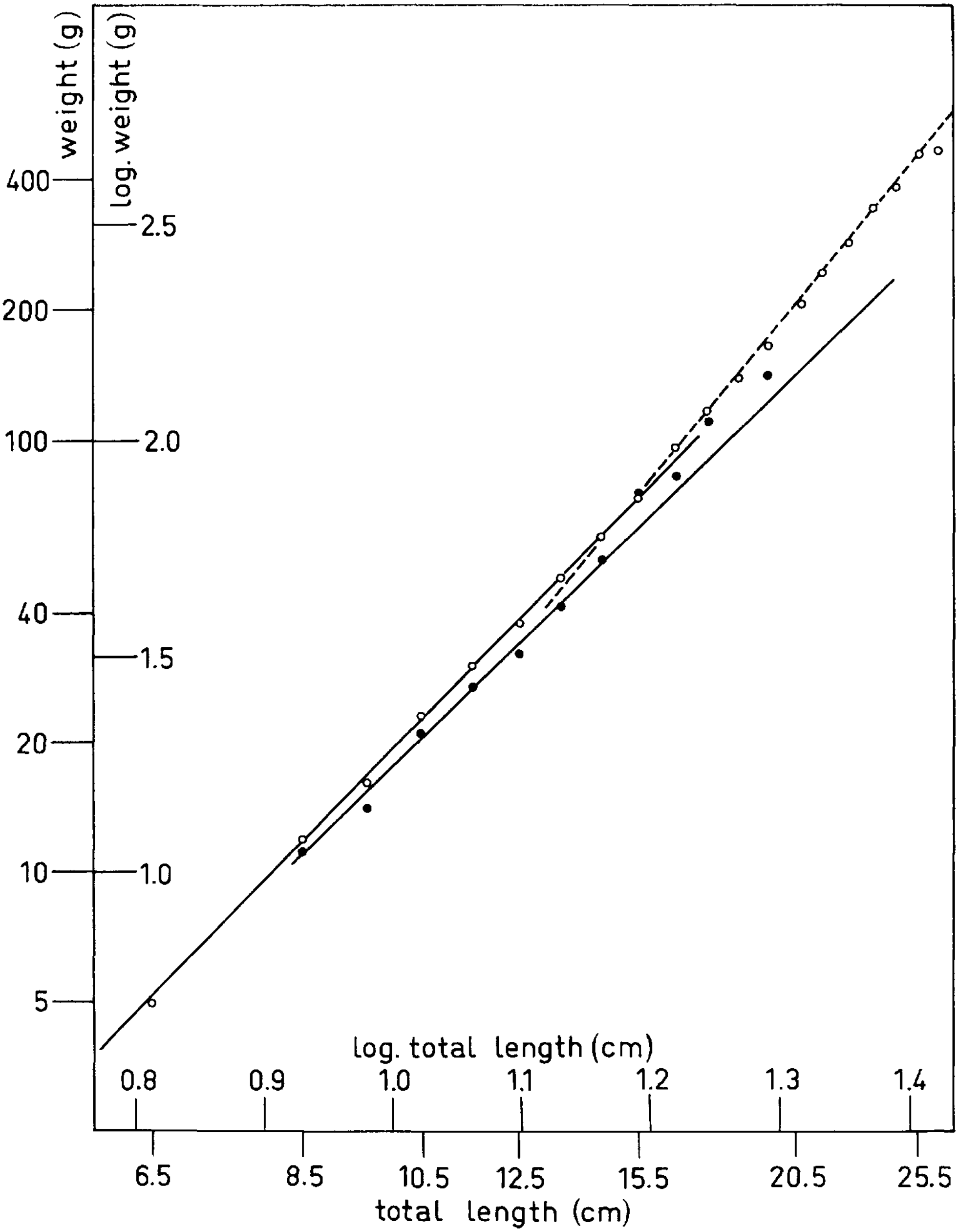

Fig. 10. Logarithm of the mean weight in cm-groups of total length plotted against the logarithm of the central value of these groups (recorded total length plus 0.5 cm; cf. p. 266 and Table 24, p. 294); males (o) and females (●). The regression lines were fitted by eye.

Table 24. Mean weights in cm-groups (grams).

Length	Males		Females					
			Non-berried		Berried		Soft	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
26	1	463	..	..	..	..	..	..
25	10	457	..	..	..	..	..	..
24	7	384	..	..	..	..	..	..
23	12	346	..	..	..	..	..	..
22	12	286	..	..	..	..	..	..
21	20	244	..	..	..	..	..	..
20	50	205	..	..	..	..	..	..
19	70	165	1	142	..	..	1	126
18	94	140	..	..	..	..	..	..
17	128	117	1	110	..	..	..	..
16	115	96	1	83	1	92	1	87
15	147	74	1	78	1	80	..	..
14	143	60	25	53	2	57	..	..
13	164	48	46	41	3	48	5	34
12	85	38	53	32	10	40	3	23
11	65	30	38	27	2	31	5	25
10	20	23	10	21	..	..	2	18
9	4	16	4	14	..	..	1	11
8	1	12	4	11	..	..	..	..
7	..	..	..	..	..	..	..	..
6	1	5	..	..	..	..	..	..

probably this is due to the relative size of the claws increasing at a higher rate above than below 15 cm. The corresponding graph of the females forms a single straight line below 15 cm, but four points corresponding to four large individuals lay above this line. This may mean that these large females have not moulted during the last two years (cf. p. 305), but more observations are needed on this point.

On the graphs Fig. 10 mean weights for each cm group were read off. These mean weights were highly independent of local and more or less random variations and were used for calculating the weight of samples which were not weighed, but of which all individuals were measured (cf. p. 267).

The paragraphs above have dealt only with the mean weights in cm groups. Also the distribution within each cm group are of interest. As the most interesting the following groups have been selected: The 12 cm and 13 cm groups (Table 25) males and females, the berried and soft-shelled females being treated separately, and the 17 cm and 20 cm groups, males only (Tables 26 and 27).

In both the 12 cm and the 13 cm groups very few soft-shelled females are lighter than the lightest hard-shelled, and very few berried females are heavier than the heaviest non-berried ones (see Table 25). This seems to show that some of the hard-shelled individuals have not gained very much in weight since they moulted, and that some of the non-berried females are about to spawn and have already

Table 25. Distribution of the weights within the 12 cm and 13 cm groups.
No soft males are included.

Weight grams	12 cm group				13 cm group			
	Females			Males	Females			Males
	Non-berried	Berried	Soft		Non-berried	Berried	Soft	
66	..	..	..	..	..	..	..	1
64	..	..	..	..	..	..	..	..
62	..	..	..	..	..	..	..	..
60	..	..	..	..	..	..	..	3
58	..	..	..	..	..	..	..	3
56	..	..	..	..	..	..	..	6
54	..	..	..	..	1	..	..	9
52	..	..	..	..	2	1	..	20
50	..	..	..	2	2	..	..	23
48	..	..	..	..	..	..	..	32
46	..	..	..	4	2	2	..	20
44	..	2	..	4	7	..	..	21
42	1	1	..	9	9	..	..	14
40	2	3	..	12	8	..	..	5
38	3	2	..	16	1	..	2	3
36	6	1	..	15	9	..	..	2
34	7	..	..	11	4	..	1	2
32	11	1	..	7	1	..	..	..
30	12	..	..	3	..	..	1	..
28	3	..	..	2	..	..	1	..
26	3	..	1	..	..	..	..	..
24	5	..	1	..	..	..	..	..
22	..	..	..	..	..	..	..	..
20	..	..	1	..	..	..	..	..
Total	53	10	3	85	46	3	5	164

attained the weight of a berried female, or they have moulted so long ago that they have attained this weight. The distributions of the hard-shelled females may therefore be expected to show three peaks: one near the weight of the soft-shelled females, one near the weight of the berried ones, and one between these two. However, the samples are too small to show these three peaks, but there is some indication of them in the 13 cm group.

The distributions of the weight of the males in the 12 cm and 13 cm groups show a simple form indicating homogeneity (see Table 25). In the 17 cm group (Table 26) the distribution is flattened with a tendency towards at least 3 peaks, and in the 20 cm group (Table 27) two peaks are obvious, one between 190 g and 210 g and one between 240 g and 250 g, and others are suggested.

This heterogeneity may be due to two phenomena. The most obvious is the age of the shell, i. e. the time since the individual moulted. While the growth in length is discontinuous, going on only at the moults, the soft parts grow continuously and also the weight of the shell increases, no doubt, during the whole of the interval between two moults. As practically all males of 12–13 cm moult once a year (about

Table 26. Distribution according to weight (grams) of males of the 17 cm group.

Weight	Frequency
162	1
160	1
158	..
156	..
154	..
152	..
150	..
148	1
146	..
144	..
142	1
140	..
138	..
136	4
134	1
132	5
130	3
128	2
126	6
124	7
122	7
120	11
118	9
116	7
114	11
112	7
110	8
108	9
106	8
104	2
102	2
100	5
98	3
96	2
94	2
92	2
90	..
88	1
Total	128

Table 27. Distribution according to weight (grams) of males of the 20 cm group.

Weight	Frequency
260	1
258	..
256	..
254	..
252	2
250	1
248	1
246	2
244	2
242	..
240	4
238	1
236	..
234	1
232	..
230	..
228	1
226	..
224	..
222	1
220	1
218	2
216	1
214	..
212	1
210	1
208	..
206	2
204	2
202	2
200	3
198	1
196	2
194	1
192	3
190	1
188	2
186	..
184	1
182	1
180	1
178	..
176	..
174	2
172	2
170	1
Total	50

May, cf. p. 304) one must expect the homogeneity of the distributions of weights in these size groups, but the larger males do not moult every year, and, therefore, their weights must be expected to gather in groups according to whether they have moulted this year, last year, or the year before, and, no doubt, that is the cause of part of the heterogeneity of the distribution according to weight of the males in the higher cm groups.

During the main moulting time also the lower size groups may be expected to show heterogeneous distributions with one peak for those which have moulted and one for those which have not, and individual weights of large samples immediately before, during, and immediately after the main moulting period would be of great interest, because they would yield an estimate of the percentage of each size group moulting each year (cf. the fact mentioned above that Poulsen (1946) found heavier males in November than in April, immediately after moulting).

Another cause of heterogeneity of the distributions according to weight may be the size and development of the claws (individuals with two biting claws may be expected to weigh less than those with a crushing claw). As the claws take a greater share of the total weight in the higher size groups their variation must be expected to cause more heterogeneity in the distributions within these groups.

Morphology of the claws

Crushing claw and biting claw.

As a rule the right and left claws of *Nephrops* are not alike, one being larger and developed as a "crushing claw" with a few large "teeth", and the other, the "biting claw", smaller without large "teeth" (cf. Fig. a, plate VI). Exceptionally both claws are biting claws (Fig. 11).

In a few cases samples were analysed as to the frequency of individuals having the right, the left, or none of them developed as a crushing claw. The result is given in Table 28, which shows that as a rule right-handedness is a little more frequent than

Table 28. Frequency of *Nephrops* having the right, the left, or none of the claws developed as a crushing claw. Samples from Faeroe waters 1937. St. 5658 and 5706 from Kalbak Fjord, 5692–5693 and 5711 rom Sundene North of the Stream, and 5707 from Sundene West of Fleserne. The table gives the number of individuals having the indicated claw developed as a crushing claw.

St.	Right	Left	None	Total
Males				
5658	95	80	10	185
5706*)	138	123	15	276
5707	166	122	28	316
5711 (2)	70	104	1	175
Females				
5658	21	20	3	44
5706*)	0	3	0	3
5707	20	26	16	62
5711 (2)	28	25	4	57
Sex not recorded				
5692–5693	279	264	42	585
5711 (1)*)	159	139	41	339

*) Only individuals $\geq$ 16 cm.

left-handedness, and in about 5–10 % both claws are biting claws, but some of the samples deviate significantly from the bulk, showing that some factor(s) may influence the relative frequencies: treated as a 3×4 contingency table the frequencies of the males result in $\chi^2 = 20.9$, df. = 6, $P < 0.005$, but if 5711 (2) is left out $\chi^2 = 4.8$, df. = 4, $0.3 < P < 0.4$. Leaving out 5706 the 3×3 contingency table of the females results in $\chi^2 = 12.2$, df. = 4, $0.025 > P > 0.01$, a significance obviously due to the

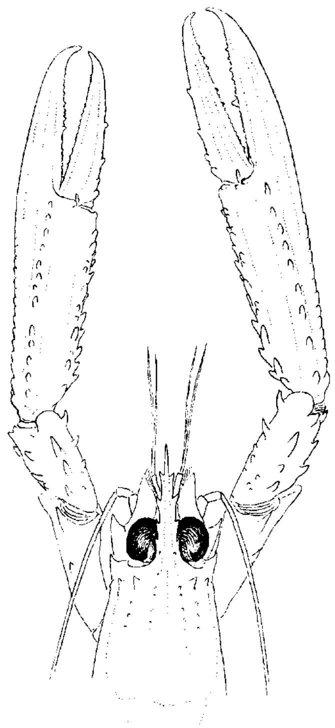

Fig. 11. Anterior part with claws of a male of 16.1 cm total length. Both claws are "biting claws" with small teeth. The left one has perhaps been lost and regenerated.

high frequency of two biting claws in St. 5707. As nothing can be said as to the cause of the non-chance deviation of the relative frequencies in the males of one sample and in the females of another, it is meaningless to state relative frequencies common to all samples from the Faeroes.

Number of tubercles on the claws.

The above analysis of the frequency of the right or left claw being the crushing claw was made in order to find some quantitative character which might show racial variation.

For the same purpose the attention of Dr. Tåning was directed towards the variation in the number of tubercles on the claws, and in two samples the tubercles in the medio-dorsal row were counted (cf. Fig. a, Plate VI). The results were noted as frequency distributions (obviously normal) for the right and left claw separately,

Table 29. Number of tubercles in the medio-dorsal row on the claws in two samples of *Nephrops* from the Faeroes 1937. (St. 5707: Sundene West of Fleserne and St. 5692–5693: Sundene North of the Stream).

St.	Sex	Crushing claw	Claw counted	Number of observations	Mean $\bar{x}$	Variance s^2
5707	♂	right	right	166	10.13	2.04
–	♂	right	left	166	9.92	2.05
–	♀	right	right	20	9.65	2.66
–	♀	right	left	20	9.20	1.54
–	♂	left	right	122	9.97	1.98
–	♂	left	left	122	10.16	2.25
–	♀	left	right	25	9.60	2.00
–	♀	left	left	26	9.27	2.12
–	♂	none	right	28	9.82	2.08
–	♂	none	left	28	10.25	3.01
–	♀	none	right	16	9.87	1.58
–	♀	none	left	16	10.06	2.20
			total...	755	10.02	2.13
5692–5693		right	right	150	10.15	1.56
–		right	left	150	10.11	1.85
–		left	right	150	10.07	1.93
–		left	left	150	10.33	1.79
....		none	right	31	11.23	2.38
–		none	left	31	11.26	4.46
			total...	662	..	..

the observations being further partitioned as to whether the right claw, the left one, or none of them was the crushing claw, and in one of the samples also as to sex. The number of observations, the mean, and the variance of these distributions are shown in Table 29.

In the sample from St. 5707, where the sex was noted, Bartlett's test for equality of the variances results in $\chi^2 = 4.20$, which for 11 degrees of freedom correspond to $0.05 < P < 0.10$ (bilateral testing), and an analysis of variance shows variances between and within the 12 groups (cf. Table 29) of 3.90 and 2.10, respectively, which results in a variance ratio of 1.86 (11 and 743 degrees of freedom, respectively) corresponding to $0.7 < P < 0.9$. This means that the number of tubercles in the medio dorsal row seems to be independent of whether the right or left claw is the crushing claw, whether the individual is a male or female, and whether the tubercles are counted on the right or left claw. It is therefore reasonable to calculate the common mean (10.02) and variance (2.13).

In the other sample (St. 5692–5693) Bartlett's test shows significant inequality of the variances ($\chi^2 = 21.45$; 5 degrees of freedom; $99.9 < P < 99.95$). However, if the 6 variances of St. 5692–5693 are tested together with the 12 of St. 5707 Bartlett's test yields no significance ($\chi^2 = 23.14$; 17 degrees of freedom; $0.8 < P < 0.9$); and, therefore, they may be chance variations of the variance common to all 18 distributions: $s^2 = 2.02$ (1399 degrees of freedom). If this is taken as an estimate of the variance within distributions an analysis of variance shows significant variation between the distributions of St. 5692–5693, the variance between distributions being 14.31 (5 df.), the variance ratio 7.08, and $P > 0.9995$. Thus it is not reasonable to calculate a common mean and variance for this sample. Obviously it is the individuals with no crushing claw that deviate in this sample as both their mean and their variance are higher. Nothing can be said about the cause of this deviation, but it should be pointed out that if the individuals with and without a crushing claw have been treated by different observers, it might result in such a difference, and in future investigations strict rules should be laid down as to the counting of "fusing" tubercles and small ones laying outside the main row.

As both the right-left localization of the crushing claw and the number of tubercles show significant, but unexplained variation, it is advisable to pay attention to the morphology of the claws during future investigations.

BREEDING AND GROWTH

MATING, SPAWNING, AND HATCHING

Review of the literature

Höglund (1942) has obviously studied the Norway lobster very thoroughly, but does not describe its behaviour explicitly; he states merely (loc. cit. p. 295) that its mating, spawning, and hatching go on in the same way as that of *Homarus*. Therefore, details on *Nephrops* behaviour cited below from Höglund are taken partly from his description of the behaviour of *Homarus* in the same paper.

Mating occurs only when the female is soft-shelled after moulting (Höglund 1942, p. 289), obviously because otherwise it offers too strong resistance against being turned over on its back by the male (Tempelman 1934, pp. 423–426).

The incubation period is about 9 months in northern waters (Storrow 1912, p. 14, Höglund 1942, p. 295) and 6–7 months in the Adriatic (Karlovac 1953, Table XI, p. 26) owing to the higher temperature in this sea (loc. cit. p. 32).

In accordance herewith *Nephrops* spawns every year in the Adriatic (Karlovac 1953, p. 34), but not in northern waters (Storrow 1912, p. 15). Here as a rule it is berried every second year, and a year elapses between mating and spawning (Höglund 1942, p. 289).

According to Höglund (1942, p. 294), Poulsen (1946, p. 37), and Karlovac (1953, p. 14) berried females are more liable to hide in their burrows than non-berried ones and males are, and Barnes & Bagenal (1951, p. 374) suggest the possibility that the females migrate after fertilization.

During egg laying the female lies on her back (Gauss-Garady 1912, p. 62, Ehrenbaum 1916, p. 89, Höglund 1942, p. 289), and when the eggs are hatching she stands frequently with her hind end elevated moving her pleopods strongly sending out clouds of newly hatched larvae (Höglund 1942, p. 290).

As to the time of spawning and hatching a number of authors note the extension of the period: Havinga (1929, p. 39) found larvae in the North Sea from April to August; Höglund (1942, p. 295) stated that in *Nephrops* spawning and hatching are more evenly distributed throughout the greater part of the year than in *Homarus*; and Bagenal (1952, p. 212) noted that planktonic larvae have been caught in the Clyde Area from April to November and that this indicates a long breeding season.

Other authors are more aware of the fact that in spite of the widely extended hatching season there is a definite maximum: Storrow (1912, p. 14) stated that at North Shields the eggs are laid in September and hatch in June; the observations of Poulsen (1946, p. 37) show that in Kattegat spawning takes place in late spring and (or) during the summer, and hatching goes on in the early spring; and according to Thomas (1954, p. 11) the main hatching season in Scottish waters appears to be in May declining thereafter in June and July; his Table 7 (loc. cit.) shows that although larvae may be caught from March to October there is a very definite concentration in May. In the Adriatic, female *Nephrops* are berried from July to February (Karlovac 1953, Table XI, p. 26) and accordingly hatching reaches its maximum in January (loc. cit. p. 31 and Fig. 13, p. 32).

Time of mating, spawning, and hatching in Faeroe waters

A rough estimate of the time of mating, spawning, and hatching in Faeroe waters may be gained from Table 30 below when Table 10 (p. 278) and the review above are kept in mind.

In Table 30 all females found in the representative samples from all catches from 1937 and 1939 have been broken up in 4 columns according to whether they were soft-shelled, hard-shelled and non-berried, berried with newly laid (green) eggs, or berried with brown eggs from the preceeding year or filaments from newly hatched eggs, and in 4 rows according to the localities and dates: Skaale Fjord, Sundene North of the Stream, all other localities in July, and these latter localities in August.

Skaale Fjord has a threshold, and the spring increase of its temperature is known to lag behind that of ordinary fjords and other Faeroe waters. Therefore, the biological processes in this fjord may be expected to lag behind, too. Also Sundene North of the Stream is guarded by a threshold, but a certain amount of water runs through it through the narrow and shallow "Stream" (Strømmen); the biological processes here may therefore be expected to be behind those of the ordinary fjords, but ahead of Skaale Fjord.

In order to evaluate the table it is necessary to consider that all females are not equally liable to be caught by the trawl: 1) Berried females lead a more secluded life (cf. p. 321), except 2) during spawning, when the female is lying on her back on the bottom (cf. p. 300), and 3) during hatching of the eggs, when the female exposes herself sending the larvae out into the water (cf. p. 300). Also 4) the moulting of the female must occur on the surface of the bottom, because otherwise mating

Table 30. Distribution according to 4×4 categories of all female *Nephrops* found in the representative samples examined in 1937 and 1939. The table gives the frequency distribution (in percentages) of the total number of females examined from each locality and month.

Locality	Date	Soft-shelled	Hard-shelled non-berried	With newly spawned green eggs	With old brown eggs or filaments of hatched eggs	Total number
Skaale Fjord	3/8	19 %	25 %	13 %	43 %	293
Sundene North of the Stream	6-20/8	17 %	80 %	3 %	0 %	401
Other localities	10-28/7	19 %	58 %	22 %	0 %	619
Other localities	3-28/8	13 %	69 %	19 %	0 %	681

could not be accomplished, and 5) immediately after the shell has hardened the female may be expected to be particularly active in the search for food. Therefore, category 1. is under-represented in the samples and the categories 2.–5. are over-represented as compared with hard-shelled, non-berried females, which have moulted long ago.

However, Table 30 shows clearly that in Skaale Fjord hatching is in full swing at the beginning of August, and some of the females that have been berried during the preceeding winter have already moulted, which means that mating is going

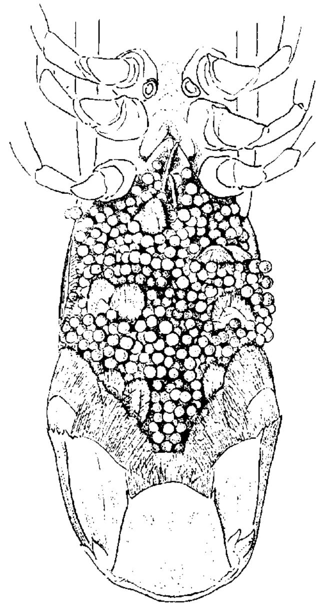

Fig. 12. Ventral view of the abdomen of a berried female.

on. At the same time spawning has started and 13 $^0/_0$ of the examined females are berried with newly laid, green eggs.

At the "other localities" hatching has finished before July, and practically all females berried the preceeding winter have moulted. Females carrying old, brown eggs or remains (filaments) of egg masses were never found in July and August in the representative samples from these localities, and only once (in Kalbak Fjord 28. July 1937) 6 females carrying brown eggs were observed in the catches.

From Table 10 (p. 278) it is known that at the "other localities" hatching is in full swing before the middle of May. Samples from these localities in May may therefore be expected to display a similar picture to that from Skaale Fjord in August.

Sundene North of the Stream may be expected to be intermediate between Skaale Fjord and "other localities", and the high percentage of hard-shelled, non-berried females is due, no doubt, to the fact that the bulk of the females berried the preceeding winter has just moulted and is therefore actively searching for food. Thus the percentage of soft-shelled females and females berried with green eggs may well be bigger in Sundene North of the Stream than in Skaale Fjord, the smaller

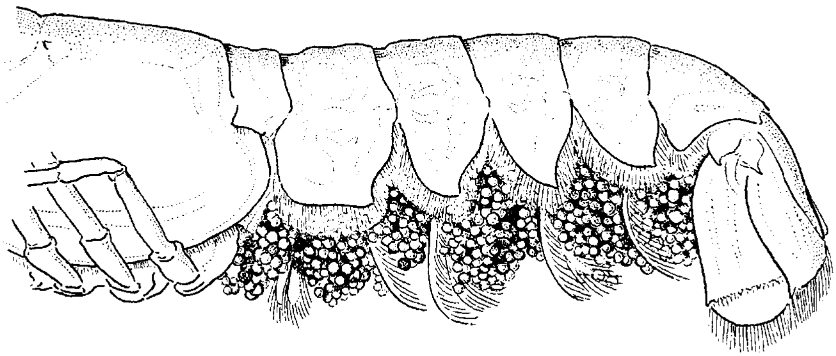

Fig. 13. Lateral view of the abdomen of a berried female (same specimen as fig. 12).

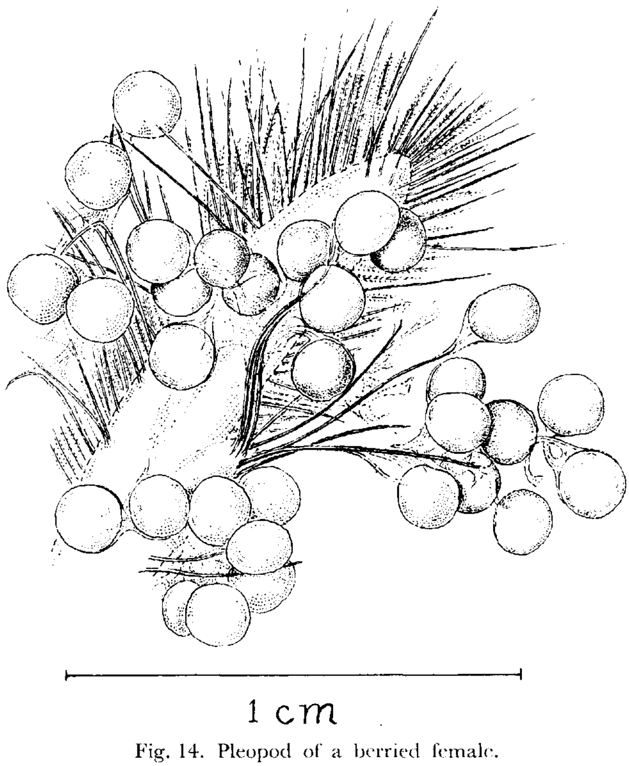

Fig. 14. Pleopod of a berried female.

frequency in the sample being due to over-representation of the hard-shelled, non-berried females which have recently moulted.

An alternative interpretation may be given of the fact that hatching and spawning coincide in Skaale Fjord, but seem to be well separated in Sundene North of the Stream: Skaale Fjord has a threshold and is also well guarded otherwise, and, therefore, its hydrography depends on the local meteorology (above all strong winds from certain directions), which may vary considerably from year to year.

As the hatching time is mostly dependent on the temperature last year and the spawning on the temperature this year, the coincidence of hatching and spawning in Skaale Fjord may well be peculiar to this fjord this particular year, and it may well be the rule that the two processes are practically separated in time as indicated by the samples from Sundene North of the Stream.

Summing up the two-years breeding cycle of the female *Nephrops* in Faeroe waters may be described as follows:

The soft-shelled newly moulted females mate in June. During this time and immediately after hardening of the shell, when they are actively searching for food, the females are very liable to be caught in the trawl.

The following year spawning goes on in June to August. As it takes place on the surface of the bottom the female is liable to be caught during this time, but during most of the following 7–9 months it will be under-represented in the trawl owing to its secluded life.

However, in May the next year (that is nearly two years after mating) the female *Nephrops* is again exposed to trawling, for now the eggs are hatching, and the female is on the surface of the bottom waving her pleopods and sending clouds of pelagic larvae up in the water. Also during the short time that elapses between hatching of the eggs and moulting of the mother, she is exposed to trawling, being actively searching for food for building up before moulting.

In June the female *Nephrops* moult and mate again, and the two-year cycle is completed.

The dates given above apply to the bulk of the population, but it must be remembered that deviations are common, and single individuals may deviate 3 months or more from the mean.

GROWTH

Growth of larvae and adolescents

An estimate of the rate of growth during the first year may be reached in the following way: In Kalbak Fjord the larvae hatch about the middle of May (cf. Table 10, p. 278). About the middle of August (cf. Table 11, p. 281) they have developed into postlarvae of about 17 mm length (15–23 mm), and, no doubt, the adults of 35–48 mm captured at the same time represent the next year group, $1^1/_4$ years old (cf. Figs. e, f, h, and j of plate V, and c of plate VII). In about 2–3 years from that time they may be expected to have reached maturity at a length of 8–10 cm.

Moulting time of the mature Nephrops

Whereas the small *Nephrops* moult many times a year, the mature males moult only once a year, as a rule (cf. p. 306), and the mature females not more than once every second year. As mentioned above (p. 304) the females moult in June.

Some idea of the time of moulting of the males may be gained from Table 31. It shows that soft-shelled males were rather common in Skaale Fjord, but very rare in the other localities. At the beginning of August Skaale Fjord has reached a stage corresponding to that of other localities in May (cf. p. 302). Therefore, it may be concluded that the moulting of the males in these localities takes place in the spring and has practically finished at the beginning of July. Compared with those at North Shields the Faeroe males seem to moult about a month later (cf. Storrow 1912, Table VII, p. 31, and 1913, Table III, p. 12).

Table 31. Percentage of soft-shelled males in Skaale Fjord and other localities.

Localities	Date	Number examined	Percentage of soft-shelled
Skaale Fjord	24. July–3. August	517	9.7 $^0/_0$
Other localities	9.–31. July	1683	0.42 $^0/_0$
Other localities	3.–25. August	2592	0.27 $^0/_0$

Interval between moults

Review of the literature.

Storrow has shown that as a rule the male *Nephrops* moults only once a year. From his two tables (Storrow 1912, Table VII, p. 31, and 1913 Table III, p. 12) it appears that there is a definite maximum of the frequency of moulting males in February to April (37 $^0/_0$ in all) and during the rest of the year only 5.7 $^0/_0$ in all were soft (a mean per month of 0.6 $^0/_0$).

As we do not know how long the males are soft after moulting we cannot know whether they all moult each year (if they are not soft more than 12 days Storrow's frequencies account for the whole of the population).

Based on studies of the epizoic barnacles (*Balanus crenatus* Brug.) on *Nephrops* Barnes & Bagenal stated that all *Nephrops* moult each year. They found that apart from the size groups 17–18 and 20–21 cm no *Nephrops* in the Clyde area carried barnacles more than one year old. They find that "this suggests that in any size-group a *Nephrops* moults at least once a year".

This conclusion is valid, no doubt, for the bulk of the male population, but their data suggest that some of the larger males moult every second year, as they found that in July 1950 2 $^0/_0$ of all *Nephrops* carried barnacles settled in the spring 1949. These *Nephrops* were males of the size groups 17–18 and 20–21 cm. Their shells were more than one year old, and they may well be fully two years, because it is not known whether the shell is attractive to barnacle settlement before it is some months old.

Furthermore their Table II (loc. cit. p. 373) indicates that more than one moult a year may be common in the smaller individuals, but it is possible to give an alternative interpretation of the fact that the smaller size groups are free of barnacles, viz. as a result of their more concealed life.

As to the females Storrow (1912, Table VIII, p. 31) has shown that the moulting period is more extended, viz. over 5–6 months, May–June to October, and during this time a total of 35–37 $^0/_0$ was found soft or recovering from casting. From the breeding cycle (cf. p. 304) we know that the mature females moult every second year. Therefore, it may seem curious that the same total percentage was found moulting in the females as in the males, but, no doubt, this is due to the fact that the moulting females are over-represented in the samples as compared with other categories of females.

(In old *Homarus* Templeman (1934, p. 430–431) found that two years may elapse between mating and spawning; later (Templeman 1936, p. 226) he concluded that "in the case of the very large females with slow growth it is quite possible that several batches of eggs may be laid and fertilized between successive moults by sperm from a single copulation". By analogy it cannot be excluded that large female *Nephrops* moult with an interval of 3 years or more).

Table 32. Occurrence of moulting in recaptured marked *Nephrops* during about one year of liberty.

Locality	Date of marking	Date of recapture	Size at recapture	
			Moulted	Not moulted
Kalbak	$^{26}/_{7}$–$^{2}/_{8}$ 1937	$^{7-12}/_{5}$ 1938	♂ 14 cm	♀ 13 cm
–	–	–	♂ 15 cm	♂ 13 cm
–	–	–	♂ 15 cm	♂ 13 cm
–	–	–	♂ 15 cm	♂ 16 cm
–	–	–	♂ 17 cm	
–	–	–	♂ 17 cm	
–	–	–	♂ 17 cm	
Sundene	$^{24}/_{7}$–$^{4}/_{8}$ 1937	$^{12}/_{5}$ 1938	♂ 15 cm	
....	–	–	♂ 16 cm	
Kalbak	$^{7-12}/_{5}$ 1938	$^{13}/_{7}$–$^{20}/_{8}$ 1939	♀ 15 cm	♂ 16 cm
–	–		♂ 16 cm	♂ 17 cm
–	–		♂ 17 cm	
–	–		♂ 18 cm	
Sundene	$^{12}/_{5}$ 1938	$^{11}/_{7}$ 1939	♂ 19 cm	
Total number	..	..	13 ♂♂ 1 ♀	5 ♂♂ 1 ♀

The conclusion drawn by Barnes & Bagenal (1951, p. 373) that all *Nephrops* moult at least once a year does not concern the females as they are berried most of the second year between two moults, and Barnes & Bagenal have examined two berried females only (loc. cit. Table III, p. 374).

Interval between moults in Faeroe waters.

Results from marking experiments.

During the first half of May 1938 marking according to size groups was carried out in Kalbak Fjord and Sundene West of Fleserne. At this occasion a number of *Nephrops* marked in 1937 was recaptured, and a number of those marked in 1938 was recaptured in 1939 (cf. fig. 4). These prawns had been about one year in the sea after marking, and although few (21 in all) they give some idea of the interval in time between moults.

In Table 32 they are separated in two columns according to whether they have moulted or not, and their sex and size at recapture are given together with the dates of marking and recapture.

The table shows quite definitely that not all *Nephrops* moult each year, and this conclusion is borne out by the fact that 3 males (of 15, 19, and 21 cm) had not moulted although they had been 2 years in the sea since marking. They were marked in Kalbak Fjord 26. July–2. August 1937 and recaptured 11. July–20. August 1939. From Table 32 it seems that about three quarters of the adult males moult each year.

Age of epifauna.

In 1937 four *Nephrops* were preserved because they had an exceptionally rich epifauna. (Details of a fifth specimen are shown in Figs. 15 and 16). They are described below. (The epifauna was identified by Dr. phil. P. Kramp, Cand. mag. K. Stephensen, Professor, Dr. phil. G. Thorson, and the author).

♂ *16 cm*, Faeroes 1937 (exact locality and date unknown). The telson, the

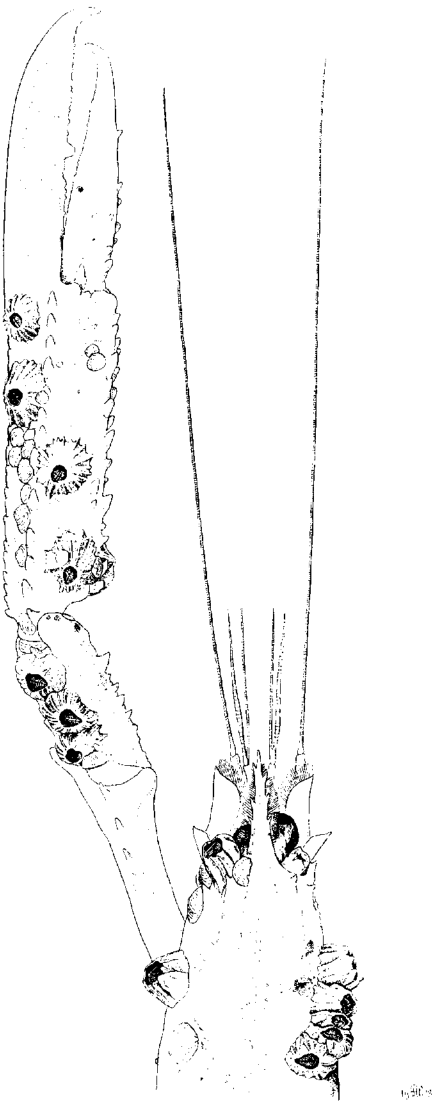

Fig. 15. Epifauna. *Balanus balanus* (L) and *Anomia squamula* L.

posterior segments of the abdomen, and the basal segments of the pereiopods were densely covered with *Hydractinia carnea*. The remaining parts of the animal were covered with *Triticella pedicellata*. The age of the individuals of these two species could not be estimated.

♂ *17–18 cm*, Arne Fjord $^{23}/_{7}$ 1937 (exact measurement impossible owing to lack of rostrum). This animal carried the following epifauna: 71 *Balanus balanus*, 1 *Anomia squamula* (6 mm), and 1 *Saxicava rugosa* (4 mm) on the left anterior pereiopod with the crushing claw; 43 *Balanus balanus* and 5 *Anomia squamula* (3–8 mm) on the right anterior pereiopod with the biting claw; 38 *Balanus balanus* and 3 *Anomia squamula* (up to 8 mm) on the dorsal part of the cephalothorax (three of the barnacles were situated in the eye cavities); 3 *Balanus balanus* and 1 *Anomia squamula* on the dorsal part of the abdomen (two of the barnacles on the telson). In all, this *Nephrops* carried 155 *Balanus balanus*, 10 *Anomia squamula*, and one *Saxicava rugosa* in addition to hydroids.

The largest barnacles measured 1 cm, and 2 out of 4 examined individuals were 3 years old judged by the number of winter rings (cf. Moore 1934), and two large

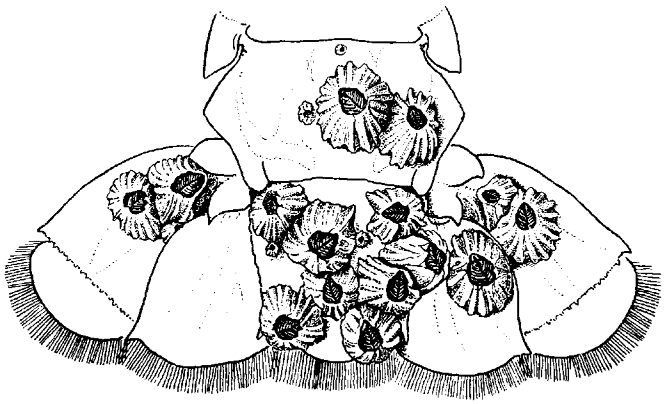

Fig. 16. Epifauna.

barnacles carried smaller ones, 0 and 1 year old, on their shells. Two *Anomia* of 8 mm were also 3 years old according to the number of winter rings.

♂ *17 cm*, Arne Fjord $^{23}/_{7}$ 1937, had 15 *Balanus balanus* and 1 *Anomia squamula* (4 mm) on the dorsal parts of the right anterior pereiopod with the crushing claw and 1 *Balanus balanus* on the ventral parts. Its right anterior pereiopod with the biting claw carried 8 *Balanus balanus* on the dorsal parts and 1 on the ventral parts. The dorsal part of cephalothorax carried 7 *Balanus balanus*, including one in each of the eye cavities, and the dorsal parts of the abdomen 1 *Balanus balanus* and 1 *Anomia squamula* (4 mm).

In all, this individual carried 33 *Balanus balanus* (measuring up to 11 mm) and 2 *Anomia squamula* of 4 mm. One of the few barnacles examined was 3 years old.

♀ *17 cm*, Faeroes 1937 (exact locality and date unknown). This female was completely covered with hydroids and bryozoans on the ventral side as well as on the dorsal side. In addition it carried 1 *Anomia squamula* (12 mm, 3 years old) on the dorsal side of the cephalothorax and 11 *Anomia squamula* (up to 8 mm) on the ventral side of the abdomen.

It will be noticed that in contrast to the males this female had a rich epifauna on its ventral side.

In all the following species were observed on the four *Nephrops* with an exceptionally rich epifauna:

Balanus balanus (L.)
Anomia squamula L.
Saxicava rugosa Lamark
Hydractinia carnea (Sars)
Triticella pedicellata (Alder).

It may be pertinent that the locality in Arne Fjord, where two of the examined *Nephrops* were fished, the bottom was partly stony, as the catch contained Laminaria and Sponges, and, no doubt, the rich epifauna on these individuals is connected with this special habitat, as epifauna is much more infrequent on *Nephrops* on soft bottom, e. g. in Kalbak Fjord and Sundene west of Fleserne.

From this examination of the epifauna the conclusion is that on more or less hard bottom *Nephrops* of 16–18 cm may live up to 3 years without moulting.

Increase in size at moult

The increase in size per moult may be estimated in two ways, viz. by direct observation of single individuals (marked or in captivity) or by size frequency diagrams.

Observing 10 individuals between 10 and 15 cm in captivity Höglund (1942, p. 295) found a mean increase per moult of 4 mm.

During the present investigation 5 recaptured *Nephrops* had moulted since they were marked according to size groups of 1 cm (cf. Table 33). They were 14–17 cm when marked and 4 of them had entered a size group one centimeter above the initial group. This seems to show that in the size interval of 14–17 cm the increase in total length per moult is about 1 cm.

In size frequency diagrams of arthropods it is often possible to read off the number of moults by the number of peaks on the graph, because all individuals which have moulted the same number of times will tend to have the same size.

In size frequency diagrams of *Nephrops* showing the total length this is impossible because the prawns can not be measured exactly enough owing to the pliability of the inter-segmental zones.

However, in 1937 the length of the carapace of 285 *Nephrops* was measured in mm (cf. Tables 16 and 17, pp. 286-288), and this material was later supplemented by measurements of 17 particularly small, preserved prawns (Table 19, p. 289).

Table 33. Increase in total length of 5 *Nephrops*, which were marked in Kalbak Fjord in May 1938 and had moulted before they were recaptured in 1939. (The males were recaptured in Kalbak Fjord, the female in Sundene).

Sex	Length at marking	Length at recapture	Increase in length	Date of recapture	Remarks
♀	14 cm	15 cm	1 cm	11/8	soft-shelled at recapture
♂	15 cm	16 cm	1 cm	19-20/8	
♂	16 cm	17 cm	1 cm	13/7	measured 18 cm when preserved
♂	16 cm	16 cm	0 cm	19-20/8	
♂	17 cm	18 cm	1 cm	12/8	

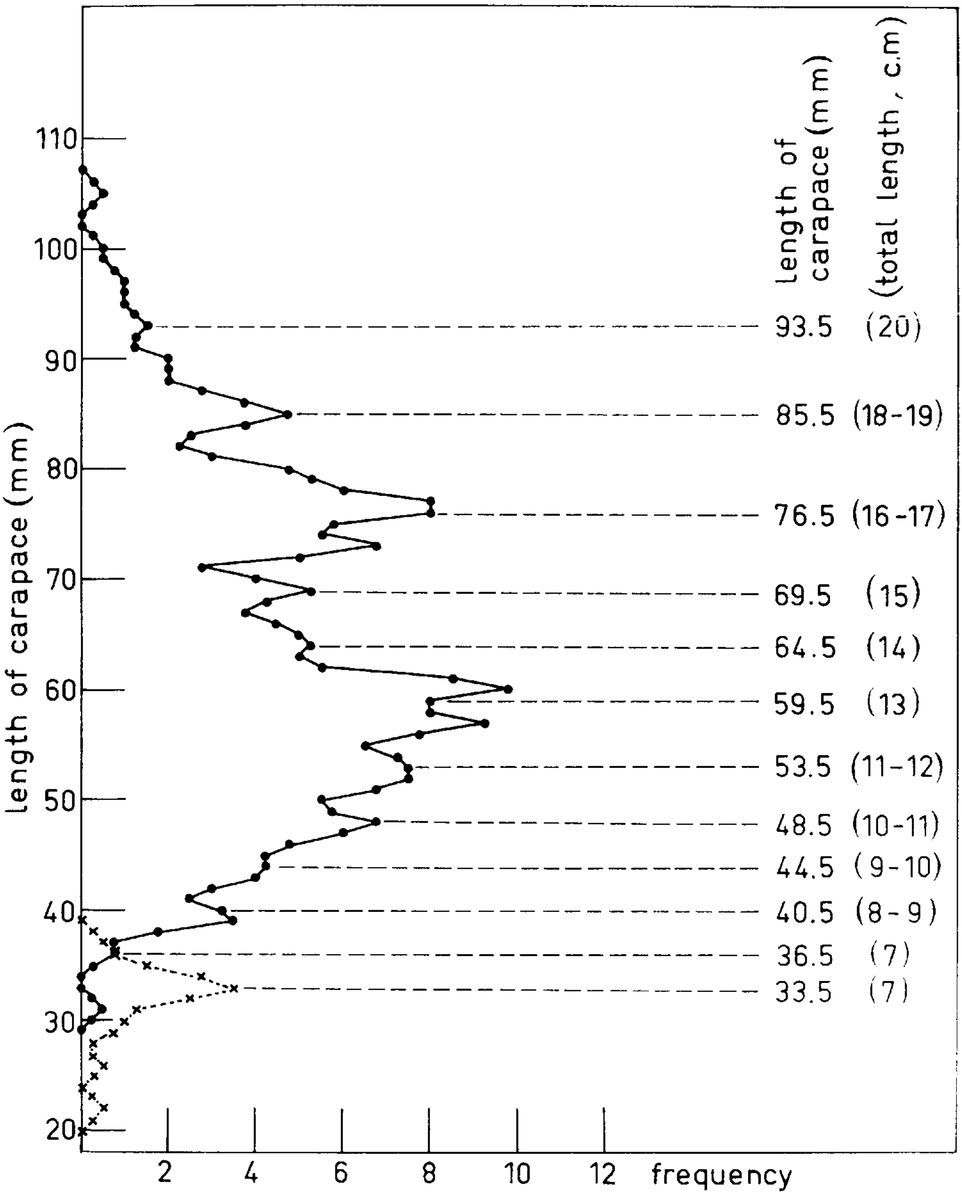

Fig. 17. Frequency distribution according to length of carapace of 285 *Nephrops* from Sundene North of the Stream (•) and 17 small specimens from Kalbak Fjord (×). The graphs have been smoothed according to the formula: (a + 2 b + c)/4 where b is the frequency in the size group in question and a and c are the frequencies in the neighbouring groups. The peaks which are supposed to represent moulting stage are marked by horizontal lines, and at each line the length of the carapace is given (in mm) as well as the corresponding total length (in cm) as read off from table 18 (p. 289). The figures for length of carapace have been corrected for downward measurements by adding 0.5 mm.

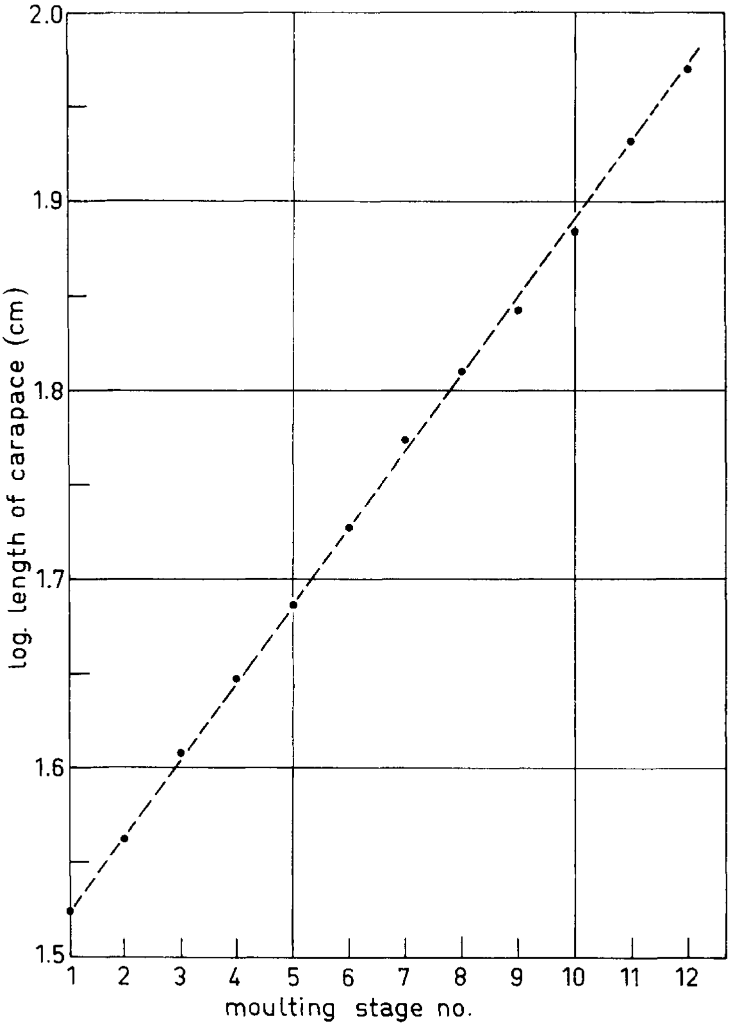

Fig. 18. The graph shows the logarithm of the carapace length corresponding to the peaks in Fig. 17 plotted against the number of the corresponding moulting stage (starting with number one for the lowest peak).

For the present purpose the measurements were used irrespective of the sex in accordance with the fact that the difference in size of the sexes is due to different numbers of moults and not to a different increase in size per moult.

Unfortunately the number of measurements is too small for the moults to be easily detectable from the distributional diagram. However, they seem to be more easily read off when the graph is smoothed using the formula $(a+2b+c)/4$, where b is the frequency in the size group in question and a and c are the frequencies in the neighbouring groups. Fig. 17 shows the smoothed graphs. The peaks which are supposed to represent moulting stages are marked by horizontal lines, and at each line the length of the carapace is given (in mm) as well as the corresponding total length (in cm) as read off from table 18 (p. 289). The figures for length of carapace have been corrected for downward measurements by adding 0.5 mm.

In order to test whether the sizes read off from the graphs represent moulting stages "Dyar's law" may be used in the form presented by Teissier (1936, p. 335). It states that in arthropodes the logarithm of the length of a rigidly chitinized organ is a rectilinear function of the number of the moulting stage. This means that if the logarithm of the length of the carapace is plotted against the number of the moulting stages the points should form a straight line. Fig. 18 shows that this is actually the case.

Accordingly there is some reason to believe that a *Nephrops* has to pass 11 moults in order to grow from a total length of 7 cm (carapace 33.5 mm) to 20 cm (carapace 93.5 mm), and that animals of 14–17 cm grow about 1 cm at each moult; this is in accordance with observations of recaptured *Nephrops* which have moulted after marking (cf. p. 309).

Perhaps the above estimate of the growth per moult will not convince most readers, even the author is not fully convinced, but it is very difficult to reach such an estimate in any other way, and the idea is presented in the hope that in the future some student of *Nephrops* will collect a greater number of measurements (about 2000 from one place) which will allow the moulting stages to be read off from the frequency diagram without smoothing it and the result to be checked on a more solid ground.

Differential growth of the sexes and its effect on the sex ratio

Earlier work.

An adequate description of the sex ratio of *Nephrops* was given already by McIntosh (1909, Table I, p. 132 and Fig. 1, p. 135), viz. according to size groups. Unfortunately all his animals were caught during the time when the females are berried, so the mature females are under-represented in his material.

Storrow (1912, pp. 13–14) suggests the right explanation of the larger mean size of the males, viz. "a difference in the intervals between casting, which in females will be determined by the time elapsing between casting and the hatching of the young, whereas in males casting may take place annually or at less intervals."

Gauss-Garady (1912, p. 63) found in most cases 60 to 80 % females in the catches. This is obviously due to the over-fishing (loc. cit pp. 78–79), which removes the larger (male) animals. Gauss-Garady ascribes it to more females than males coming out of their tubes, especially those with eggs, and he even mentions the possibility that the berried females do not at all hide in the mud. (He does not state this as a fact, as cited by Karlovac (1953, p. 14)).

Barnes & Bagenal (1951, p. 377) state that the unequal sex ratio in the larger size groups is due to differential mortality.

Karlovac (1953, Fig. 4, p. 17) discribes the sex ratio according to size groups. In the High Adriatic he finds a female sex ratio significantly above 50 % before maturation. In both the High Adriatic and the North Adriatic Channel Region the female sex ratio is near 50 % about the onset of maturation, but from that point it increases for two size groups and then decreases passing 50 % two to three size groups later and goes on towards zero. However, Karlovac (loc. cit. p. 14) makes only a very short comment on this important diagram, and he does not

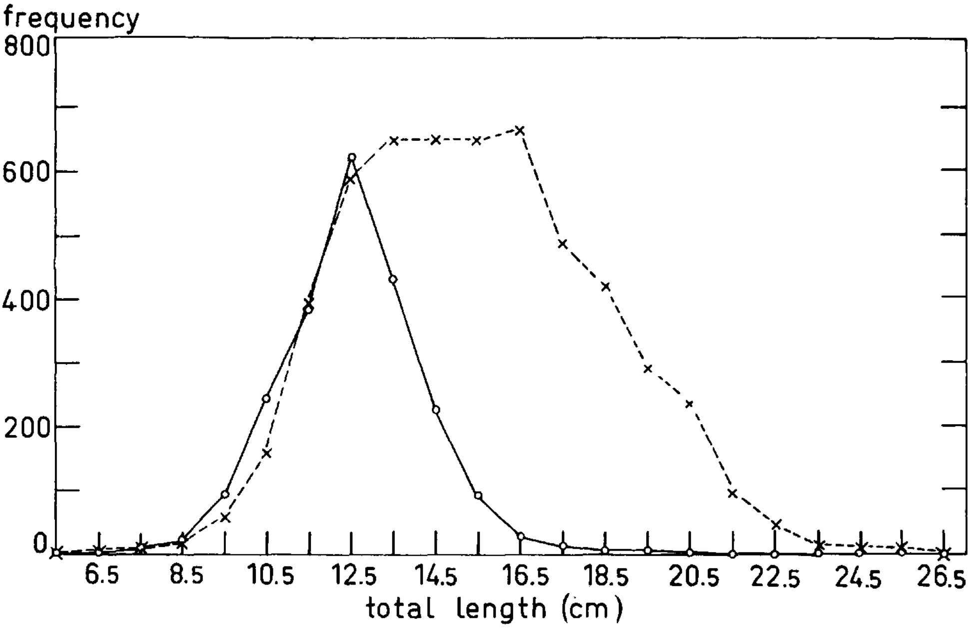

Fig. 19. Distribution according to total length of 5573 males (×) and 2159 females (o) from the Faeroes 1937 and 1939. (The same material was used for the calculation of Fig. 20).

draw the full conclusion from it as he attributes its shape to a higher mortality as well as a slower growth of the females.

Also Thomas (1954, Table 5, p. 7) describes the sex ratio according to size groups and finds significantly more females than males in the immature groups, but unfortunately the mature females are under-represented in his material, which is from September, when about half of them are berried. He notices that the female sex ratio decreases with increasing size and attributes this to a surplus reduction in the moulting frequency in the females as compared with the males (loc. cit. p. 9).

Own investigations.

At an early stage of the investigations of the Faeroe *Nephrops* it became clear that the female sex ratio varied between 0 % and 50 % from catch to catch, and that it varied inversely with the percentage of large prawns (≥ 16 cm). This is obviously due to the fact that almost all females are under-sized (see Fig. 19), and as they show almost the same sensitivity to light as the males (apart from the berried ones, which are more sensitive), the female sex ratio must decrease when the percentage of large prawns increases with the intensity of the light (cf. p. 319).

Obviously the sex ratio can be adequately described only if it is calculated for size group (e. g. of 1 cm). The graph Fig. 20 shows the result of this calculation. Immature size groups (<8 cm) are so insufficiently represented that nothing known of their sex ratio. From the onset of maturation (at 8–9 cm; the smallest

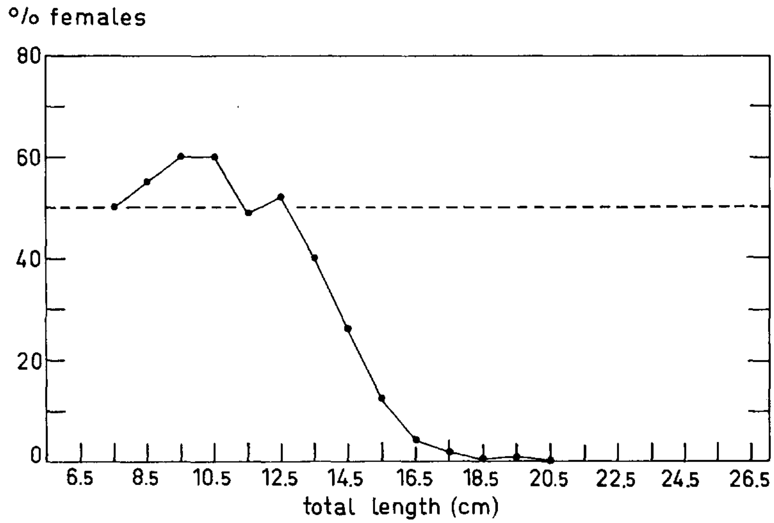

Fig. 20. Percentage of females as a function of total length, based on the same material as Fig. 19, from which confidence limits may be estimated.

berried females were 9 cm) to a size of 11–12 cm the female sex ratio is above 50 %, but with increasing size it decreases gradually to 0. A similar graph (Fig. 21) has been calculated from the measurements published by Storrow (1912).

Assuming that at the onset of maturation the sex ratio is 50 %, and further (with Storrow, loc. cit.) that the smaller size of the females is due to their less frequent moulting connected with spawning, it is obvious that the graph must have the shape shown in the Figs. 20 and 21: After maturation the females can not moult more frequently than every second year, whereas the males may moult every year. Owing to this inhibition of the growth of the females as compared with the males there must be more females than males in the size groups immediately above the point of maturation (the males "grow away" from these size groups). However, with increasing size the females must die off more quickly, because the females of a certain size are older than the males of the same size.

It has already been mentioned (p. 312) that Karlovac (1953) gives graphs of the same shape, especially the surplus of females is noticed in the size groups just above the maturation point. McIntosh (1909) and Thomas (1954) did not find this because their samples were exclusively from the season when about half of the females are berried and therefore under-represented in the samples (cf. p. 312 and 313).

The material collected at the Faeroes does not give any information of the se ratio before maturation. However, Karlovac (1953) and Thomas (1954) found female sex ratio above 50 % in the immature size groups. This seems to sh that already at the immature stages the males moult more frequently and g faster than the females.

The fact that Karlovac (loc. cit.) finds a return of the sex ratio to about at the maturation point seems to show that males mature at a smaller siz

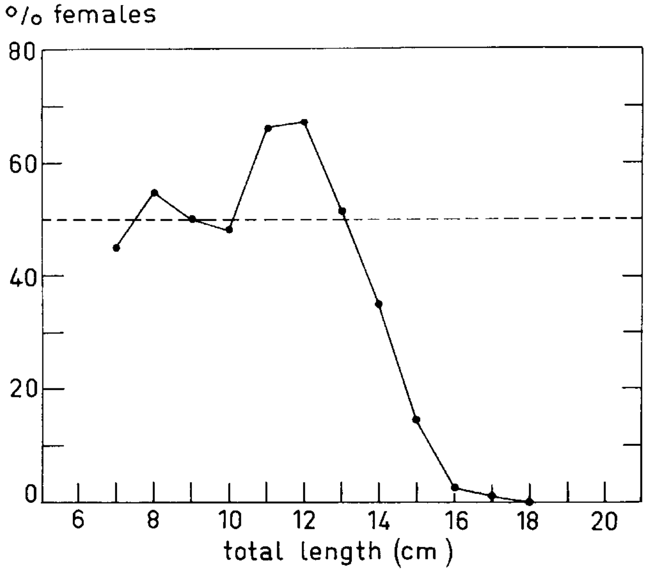

Fig. 21. Percentage of females as a function of total length for 5650 males and 2036 females from the North Shields based on the observations of Storrow (1912).

the females. From that point onwards the males may be supposed not to moult more than once a year, whereas presumably the females continue to moult more frequently until they mature at a stage about one size group larger.

FOOD AND ENEMIES

FOOD

Very little has been published on the food of the Norway lobster. Höglund (1942, p. 294) has studied the contents of its stomach, but found only unidentifiable fragments of shells of bivalves and small crustaceans, because most food was finely crushed, but in captivity he was able to feed it with fish of all sorts, shelled mussels, shrimps, and small crabs, and he concluded that its natural diet is likely to show great variation.

Also Gauss-Garady (1912, p. 62) kept *Nephrops* in captivity and states that it eats everything, but prefers carrion. He caught it in traps baited with carcasses of the crab, *Portunus depurator.*

Contrary to this Ehrenbaum (1916, p. 90) states that in captivity the Norway lobster hardly touches the flesh of fish or mussels offered as food.

In view of our scanty knowledge on this point some interest may be attached to the analysis of the contents of the stomachs of 13 *Nephrops* caught in Kvannesund 25. August 1937, 22^{35}. The result was:

♀ 10 cm, berried: 1 mandible of a nereid.
♀ 11 cm, soft after moulting: 1 operculum of *Margarita ?groenlandica.*
♀ 12 cm, soft after moulting: empty.

♀ 11 cm, berried: 1 mandible of a nereid.
♂ 13 cm: fragments of shells of *Syndosmya nitida* and other molluscs.
♀ 12 cm: 2 foraminifers.
♀ 10 cm, soft after moulting: 3 foraminifers.
♀ 10 cm, berried: 3 mandibles of nereids, 2 foraminifers, *1 Onoba striata*, fragments of calcarious shells.
♀ 12 cm: 1 scale of ?*Lepidonotus* sp.
♂ 12 cm: 1 foraminifer, much unidentifiable material.
♀ 12 cm: fragments of shells of *Tellina fabula* and *Nucula* sp.
♂ 15 cm: 1 radiolarian, fragments of shells and other unidentifiable material.
♂ 14 cm: unidentifiable material.

To round up the following systematic categories may be listed as present in the stomachs (identified by Professor, Dr. phil. G. Thorson and the author):

foraminifers
radiolarians
polychaetes
  nereides
  ?*Lepidonotus*
lamellibranchs
  Syndosmya nitida (Müller)
  Tellina fabula Gronovius
  Nucula sp.
prosobranchs
  Margarita ?groenlandica
  Onoba striata (Montagu)

Everything found in the stomachs was heavily digested and a brown, fluffy mass ("detritus") was in all cases the dominating contents. As *Nephrops* feeds at night, there can be no doubt that samples taken at night or in the morning will yield a better result, and the stomachs should be taken immediately after the animals have been caught in order to prevent further digestion.

As to the fragments of calcareous shells it can not be excluded that dead shells may be eaten in order to secure calcium carbonate for moulting.

As relevant to the question of the food preference of the *Nephrops* it may be added that at the Faeroes it was caught in traps baited with cod flesh and dead *Nephrops*.

ENEMIES

Gauss-Garady (1912, p. 61) gives a long list of fish and other animals, which eat *Nephrops*. Ehrenbaum (1916, p. 90) mentions the cod as particularly important, and Bagenal (1952, p. 212) states that of a variety of stomachs investigated those of the cod were the only ones containing *Nephrops*. Also Höglund (1942, p. 295) mentions the cod as a very important enemy.

In this connection it may be of interest that *Nephrops* smaller than 5 cm were found in the stomachs of rays (*Raja clavata*) of about 50 cm caught in Kalbak Fjord 12. July 1939, 18^{20} and 20^{00}. This shows that the rays are able to capture the small *Nephrops* while it is still daylight.

REACTION TO LIGHT

EARLIER INVESTIGATIONS

Notes on *variation in the size and composition of the catches* are scattered in the literature. Gauss-Garady (1912, p. 44) states that using tow nets in the Adriatic the fishermen get larger catches at night than by day. Storrow (1912, p. 14) notes that the percentage of females is highest during the winter, and at this time the percentage of berried females is least in the catches. Ehrenbaum (1916, p. 87) mentions that landings by German trawlers of *Nephrops* from the North Sea are most frequent during the winter. According to Höglund (1942, p. 294) the Swedish experimental fishery got the largest catches in depths of about 65 m in January, but in the following months the depth of the largest catch increased steadily to 225 m in June and then decreased gradually until the next January. Poulsens (1946, Table 2, p. 33) data show a smaller mean size of the Nephrops in June than in November–December and a still smaller in April, but Barnes & Bagenal (1951) found a smaller percentage of large *Nephrops* ($\geq$ 16 cm) in June–August than in October and January (cf. Table 34).

Karlovac (1953) found no definit tendency towards a higher mean size during the summer than during the winter (loc. cit. Table VIII, pp. 21–24), but he shows in the most admirable way (loc. cit. Fig. 3, p. 14) that the berried females are under-represented in the catches as compared with the non-berried ones and the males, and that this results in a yearly variation in the sex ratio in the catches.

Two different *interpretations* have been given of the variation in the catches, viz. that at certain times parts of the population either have migrated or are hiding in the mud.

Already Gauss-Garady (1912, p. 44) has given a clear description of the behaviour of the *Nephrops* in the mud. He states that during day time it digs itself completely into the mud and only during the night it comes out of its cover in order to seek food.

He reached this conclusion from the following observations: 1) His own experiments with traps. 2) The fact that (in the Adriatic) the *Nephrops* never has epifauna or epiflora on its shell, as other bottom crustaceans have. 3) The observation that newly caught *Nephrops* have mud on the small hairs on their body (this relates presumably to trapped specimens). 4) The fact mentioned above that using tow nets the fishermen get larger catches at night than by day. When they fish by day they put more lead at the lower edge of the net so that it penetrates deeper into the mud.

He states further that the smaller the *Nephrops* are the deeper they burrow into the mud, and that is the reason why *Nephrops* of 2 to 5 cm length are rarely caught in the net.

However, he also states that the *Nephrops* are particularly active in moonlight, that the small animals do not live in the same places as the adults, and that during

Table 34. Seasonal variation in the percentage of large male *Nephrops* ($\geq$ 16 cm) in the Clyde area (based on observations of Barnes & Bagenal 1951, Table IV, p. 375).

	June	July	August	October	January
Percentage of large ♂♂	50	58	46	82	85
Total number of ♂♂	127	555	280	199	39

the cold season the *Nephrops* migrate to shallow water and during the warm season to deeper water.

Storrow (1912, p. 14) does not mention migration (as stated by Thomas (1954, p. 12)), but writes that "habits of which no knowledge at present is obtainable bring about the small percentage of females in summer and of berried females in winter".

Ehrenbaum (1916, p. 88) mentions both migration and hiding as possible explanations of the under-representation of the berried females.

Höglund (1942, p. 294) finds that the annual variation in the depth of the largest catch (cf. above) indicates a migration, but adds that the question is not fully cleared up. On the other hand he has seen *Nephrops* in captivity dig themselves into soft bottom, and he thinks that this habit might be particularly pronounced in the berried females, and that is a probable explanation of the fact that they are rarely caught in the trawl.

Poulsen (1946) is most inclined to accept their hiding in the mud as the explanation of the lack of the young stages (loc. cit. p. 33) and the under-representation of berried as well as non-berried females (loc. cit. p. 37) in the catches. He states, however, (loc. cit. p. 33) that perhaps it can not be completely excluded that the young *Nephrops* live in other places than the adults, perhaps on stony bottom, where they can not be caught by any kind of seine or trawl.

Barnes & Bagenal (1951, p. 377) show a photograph of a burrow of a young *Nephrops* and admit that the smaller animals, males and females, may lead a more secluded life, and, in their opinion, this is borne out by the fact that all *Nephrops* up to 11 cm were completely free of barnacles (the present author would ascribe this to their more frequent moulting). However, they are more inclined to accept migration as the cause of variations in the composition of the catches (loc. cit. p. 374–375).

Karlovac (1953, p. 14 and 44) ascribes the annual variation in the sex ratio in the Adriatic to a more concealed life of the berried females.

Thomas (1954, p. 8) accepts the possibility of migration, but does not find it necessary for the explanation of variations in the sex ratio.

RESULTS OF THIS INVESTIGATION

During the investigation in Faeroe waters it soon became clear that in shallow water, at depths of 30–50 m, trawling during the day gave comparatively small catches with a high percentage of large animals (> 16 cm), and during the night large catches with a low percentage of large prawns. Therefore, it was reasonable to suppose that the size and composition of the catches depended on the intensity of the light. Whereas a direct examination of this problem is excluded owing to the lack of measurements of the intensity of the light during the investigation at the Faeroes, an approximate description of the phenomenon has appeared to be possible if the theoretical altitude of the sun is used as a measure of the intensity of the light.

The theoretical altitude of the sun was calculated from 1) the longitude and latitude of the Faeroes, 2) the declination of the sun on the date in question, and 3) the time midway between the start and the end of the haul. Figs. 22 and 23 show the dependence of respectively the percentage of large animals and the weight of the catches on the theoretical altitude of the sun. The diagrams are based on observations in Kalbak Fjord in 1937 and 1939. It is obvious that at different times with equal altitude of the sun the intensity of the light may vary considerably owing to variation in the density and distribution of the clouds, the transparency of the water etc. For this reason 4 hauls taken during fog have been omitted from the diagram, and, furthermore, lines have been drawn between points representing

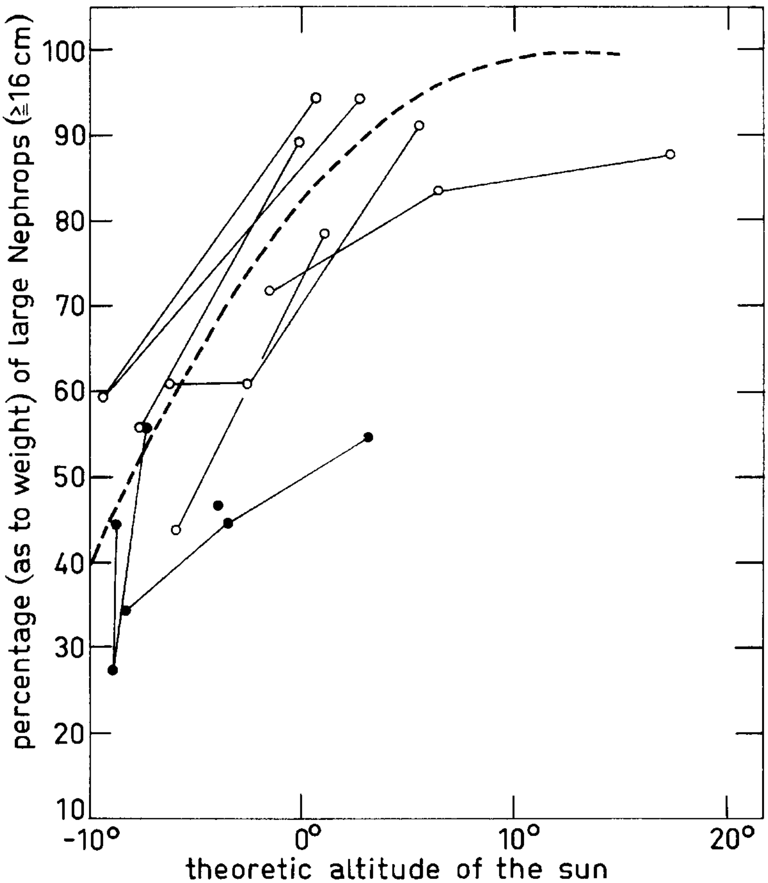

Fig. 22. Percentage according to weight of large animals (≥ 16 cm) plotted against the theoretical altitude of the sun each point representing one haul from the outer part of Kalbak Fjord 1937 (•) and 1939 (o). The broken-lined graph for "average" has been fitted by eye taking account of the inclination of the lines drawn between points representing hauls taken in immediate succession and of the fact that most errors will lower the observed values.

hauls taken in immediate succession according to the reasonable assumption that these lines give a good approximation to the inclination of the "true" graph, because the factors affecting the relation between the altitude of the sun and the intensity of the light have been relatively constant during these hauls, and they are likely to have been taken in almost the same place.

In Fig. 22 the percentage (according to weight) of large animals (≥ 16 cm) is plotted against the theoretical altitude of the sun each point representing one haul from the outer part of Kalbak Fjord. The diagram shows a steep increase of the percentage of large animals from about 40 $^0/_0$ at $-10°$ altitude of the sun to about 95 $^0/_0$ at $+6°$ altitude of the sun.

In Fig. 23 the size of the catch (kg per hour) is plotted against the altitude of the sun. In this case the deviations from the average are more striking than in the case of the percentage of sized animals owing to the fact that the size of the catch is more influenced by other factors, such as the density of the population, the working of the trawl, the speed of the boat, the wind etc. However, it is reasonable to believe

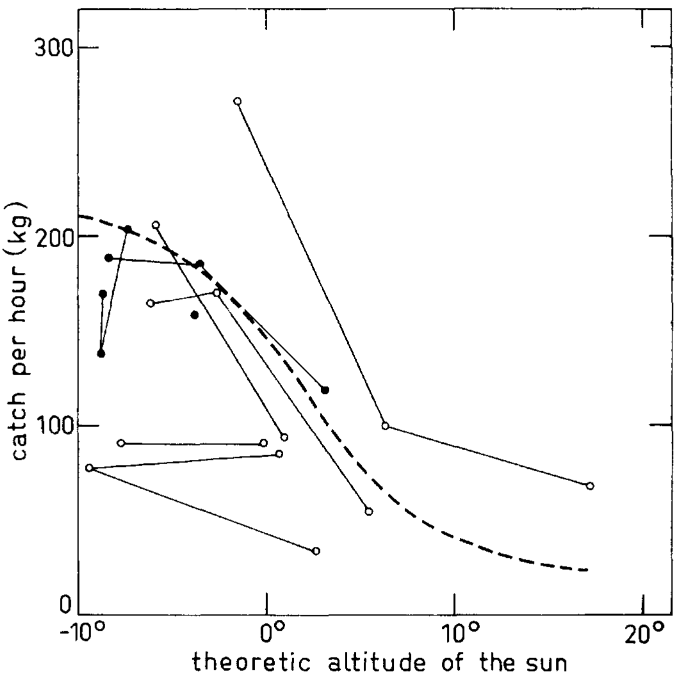

Fig. 23. Size of the catch per hour (kg) plotted against the theoretical altitude of the sun each point representing one haul from the outer part of Kalbak Fjord 1937 (•) and 1939 (o). The broken-lined graph for "average" has been fitted by eye taking account of the inclination of the lines drawn between points representing hauls taken in immediate succession and of the fact that most errors will lower the observed values.

that the broken-lined graph approximately illustrates the average when the trawl is working well. It is S-shaped, the catch decreasing from 210 kg in complete darkness ($-10°$ altitude of the sun) to about 21 kg in the brightest daylight.

Apart from Kalbak Fjord, Sundene West of Fleserne is the only place where enough hauls were taken for such an analysis to be made. However, the observations from Sundene do not show an effect of the altitude of the sun on the size and composition of the catches. This is hardly due to the greater depth (70–80 m), but rather to the fact that in 1937 fishing was mainly at night and in 1939 mainly by day, and in 1937 hauls were chiefly taken north of Kællingen and in 1939 chiefly south of Kællingen. This confounding of the intensity of the light with the years and the positions blurred the effect.

To the observations described above should be added that the sex ratio in single hauls varied from 0 $^0/_0$ to 48 $^0/_0$ inversely with the percentage of large animals, further that berried females were found only in hauls taken at very low intensity of light, and finally that it is my impression that *Nephrops* brought on the deck moved more lively at night than in daylight.

From the above observations the following conclusions may be drawn:

1) *Nephrops* of all sizes are sensitive to light in the way that they tend to hide during the day and be active during the night. This explains the larger catches at night than by day in the Adriatic (cf. Gauss-Garady above) and renders the acceptance of migration unnecessary for explaining Höglund's observations showing that the largest catch is taken on greater depth in summer than in winter, provided that fishing is done by day, and it is also in accordance with Ehrenbaum's observation (cf. above).

2) The sensitivity to light decreases with increasing size. At high intensities the larger animals only are active, but with diminishing light smaller and smaller animals become active. This is not in accordance with the observations of Poulsen (1946) and Barnes & Bagenal (1951) (cf. above), but a small variation in the time of the day of trawling may easily over-shadow the effect of the seasonal variation in the intensity of the light. Another possible explanation of this disagreement is given below.

3) Non-berried females show almost the same sensitivity to light as males of the same size, and, as almost all females are under-sized, the female sex ratio of the catches varies inversely with the intensity of the light. This is in accordance with Storrow's observation that the female sex ratio is highest in winter (cf. above). The apparent contradiction of Karlovac's results is due to the fact that the seasonal variation in the light is much smaller in the Adriatic than at Scotland.

4) Apart from the time when the eggs are being laid and when they are about to hatch berried females are much more sensitive to light than non-berried ones and males of the same size, and, therefore, they are caught only at very low intensities of light. This was also demonstrated by Karlovac (cf. above).

5) Spawning females are less sensitive to light than non-berried ones and males of the same size (cf. p. 304). This is in accordance with the graph of Karlovac (1953, Fig. 3, p. 14) which shows a provisional maximum at spawning time.

6) Berried females with hatching eggs are also less sensitive to light than non-berried ones and males of the same size (cf. p. 304). This and (5) explain why Storrow found the lowest percentage of berried females in winter.

7) Experience from Kalbak Fjord shows quite definitely that migration does not take place to any significant degree: the berried females as well as the young stages (cf. p. 277) are present in the same place as the large males, but they are caught only at very low intensities of light.

In trying to generalize the results presented in Figs. 22 and 23 it should be remembered that the observations were made exclusively during July and August when the night at the Faeroes is very short and not very dark. The whole population had to come out to feed during the few hours of night. At lower latitude or at other times of the year when the night is long, we can not be sure that the whole population is active during the whole of the night, so the difference between day and night catches need not be so striking. On the other hand when the night is very short it will be too short for feeding, so the *Nephrops* will have to come out now and then during the very long day. This may be the explanation of Barnes's & Bagenal's observations (Table 34, p. 317): in June–August the night is short and, therefore, the small animals have to come out now and then during the day, thus decreasing the percentage of large *Nephrops*, but in October and January the small animals get enough food during the long night, so only large *Nephrops* are active during the day which results in a high percentage of large prawns.

As a conclusion it may be stated that quantitatively the observations presented in Figs. 22 and 23 are "a sample of one" characterizing this particular population at this particular latitude, season, depth, transparency of the water etc., but qualitatively, on the other hand, the seven points given above should have rather general validity.

SUMMARY

From observations carried out at the Faeroes mainly in 1937 and 1939 the following conclusions are drawn.

Apart from Suderø *Nephrops norvegicus* (L.) is present in all the fjords and sounds where the bottom consists of mud.

The *density of the population* was estimated by the catch per unit effort. In properly investigated places where the bottom is invariably muddy the mean density varies between 210 kg/h in the outer part of Kalbak Fjord and 590 kg/h in Sundene at Fleserne, both figures being corrected for the effect of the light. In almost all places where the experimental fishing was less intense the catches were smaller probably owing to either partly sandy bottom or bad fishing due to obstacles.

In three places the *size of the populations and their habitats* were measured by *marking*. The total population in these places was estimated at about 380 tons and the corresponding habitats at about 1700 trawling hours, provided constant catch.

To the earlier *morphological descriptions of the juvenile stages* the only important addition concerns the postlarva which was found for the first time in greater numbers. The morphology of this stage seems to show that it moults several times. Its distribution according to size is given.

As to the *morphology of the adults* some quantitative characters are added to the earlier descriptions.

The *overall length of the adults* cannot be characterized by frequency distributions as such distributions are functions of the gear and the intensity of light during fishing (cf. below). It is therefore characterized by three figures: 1) The maximum length of the two sexes, which shows that the Faeroe Nephrops does not differ conclusively in length from other populations. 2) The minimum length of berried females caught, but as this is a function of the mesh size of the fishing gear, a better character is 3) the average length at which the female starts spawning .This may be estimated from the graphs of the sex ratio plotted against the length (cf. below). This figure also shows no conclusive difference between populations from which such graphs may be drawn.

The *relative length of the carapace* measured from the tip of the rostrum decreases steadily up to 12 cm total length, but seems to be independent of further increasing length. As a rule the females have a smaller carapace (longer abdomen) than males of the same total length. The postlarvae have a relatively smaller carapace than the smallest adults.

The *relative weight* of the *Nephrops* is illustrated by plotting the logarithm of the mean weight against the cm groups of the total length, also on a log. scale. The males follow two straight lines, one below and one above the 15 cm group, thus indicating a change in the allometry, probably the rate of increase of the claws. The males are heavier than the non-berried females, which form a straight line below 15 cm.

The distributions according to weight within each cm group show certain heterogeneities which, when followed throughout the year, may be used for studying moulting and spawning.

Two features of the *morphology of the claws* have been studied. The frequency of the crushing claw being the right or the left one is significantly different in the samples, but the reason for this is unknown. Also the number of tubercles in the medio-lateral row on the claws shows an unexplained significant variation, so a closer examination of the morphology of the claws is advisable during future investigations.

A review is given of the literature on the behaviour in connection with *mating, spawning, and hatching* and the times when they occur. A rough estimate of these times at the Faeroes is based on 1) this literature, 2) plankton samples containing *Nephrops* larvae from the Faeroes, and 3) the percentage of females which were soft-shelled, hard-shelled and non-berried, berried with newly spawned green eggs, and berried with old brown eggs or remains thereof from a threshold fjord, a less sheltered place, and the ordinary open places, the latter for July and August separately.

The conclusion is that the female *Nephrops* has a two years breeding cycle in Faeroe waters: Moulting of the female and mating occur mainly in June. Spawning goes on in June to August the following year, and the eggs hatch in May the next year, that is nearly two years after mating. This goes for the bulk of the population, but each year a minority deviates up to 3 months or more.

On the *growth* the following conclusions are drawn: The larvae hatching in May have developed to postlarvae in August, and adults of 35–48 mm caught at the same time seem to be $1^1/_4$ years old.

The mature males *moult* in the spring, the females in June. Marking experiments indicate that about three quarters of the adult male Nephrops moult each year. Four *Nephrops* had a particular rich epifauna, which showed that on more or less hard bottom *Nephrops* of 16–18 cm may live up to 3 years without moulting.

Of 5 *Nephrops* being 14–17 cm when marked and having moulted before recapture 4 had entered a size group one cm higher, thus indicating an increase per moult of about 1 cm. The same result was reached by reading off the moultings from a smoothed size frequency diagram showing the distribution according to length of the carapace, and testing the result by Dyars law. The latter method indicates 11 moults during the growth from 7 cm to 20 cm total length.

The *sex ratio* is a function of the size, and plotted against the size groups of 1 cm it shows the following picture: From the onset of maturity at about 8 cm to about 11–12 cm the females are in the majority, but above this length the female sex ratio decreases steeply and reaches zero at about 20 cm. This graph is explained by the fact that as a rule mature males moult every year, mature females every second year.

The *stomachs* of 13 *Nephrops contained* remains of foraminifers, radiolars, polychaets, and molluscs.

Among the *enemies* of the Norway lobster *Raja clavata* of about 50 cm is important at the Faeroes as many *Nephrops* of less than 5 cm were found in the stomachs of this species.

From the literature it is obvious that the *size and composition of the catches* of the Norway lobster vary seasonally and diurnally, but the picture is rather confusing. At the Faeroes it is shown quite clearly that in Kalbak Fjord at depths of 30–50 m the size of the catch as well as the percentage of large prawns ($\geq$ 16 cm) is a function of the intensity of the light. Owing to lack of measurements the theoretical altitude of the sun has been used as a measure of the intensity of the light, and graphs are given showing the size of the catches and the percentage of large prawns plotted against the theoretical altitude of the sun. They show that in full daylight one gets small catches of almost exclusively large prawns ($\geq$ 16 cm), whereas in complete darkness catches are large and with a great percentage of undersized prawns.

From these and other observations the following conclusions are drawn: All *Nephrops* are *sensitive to light*. They tend to hide in daylight and be active in darkness. The sensitivity decreases with increasing size. The non-berried females show almost the same sensitivity as males of the same size, and as, on an average, the females are smaller than the males a higher percentage of females are caught by night than by day. For most of the time berried females are more sensitive than non-berried ones, but spawning females and berried females with hatching eggs are less sensitive, and so are the soft females.

Migration does not take place to any significant degree; berried females and post-larvae are present in the same place as the large males.

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Plate V. *Nephrops norvegicus* (L.) from Faeroe Waters. External genital characters.

a. Male of 25.9 cm total length. Part of cephalothorax and of abdomen. Ventral view showing the genital openings and the modified first pair of pleopods.
b. Same as Plate V a. Lateral view.
c. Male of 16.5 cm total length. Ventral view of part of the animal showing one abnormal genital aperture (cf. McIntosh 1904 and 1909).
d. Female of 19.5 cm total length. Same view as Plate V a.
e. Female of 42 mm total length; from stomach of *Raja clavata*. Same view as Plate V a.
f. Female of 38 mm total length; from the stomach of a *Raja clavata*. First pair of pleopods.
g. Male of 54 mm total length. First pair of pleopods.
h. Male of 48 mm total length (same specimen as Plate VII c). First pair of pleopods.
j. Male of 35 mm total length; from stomach of *Raja clavata*. First pair of pleopods.

PLATE V

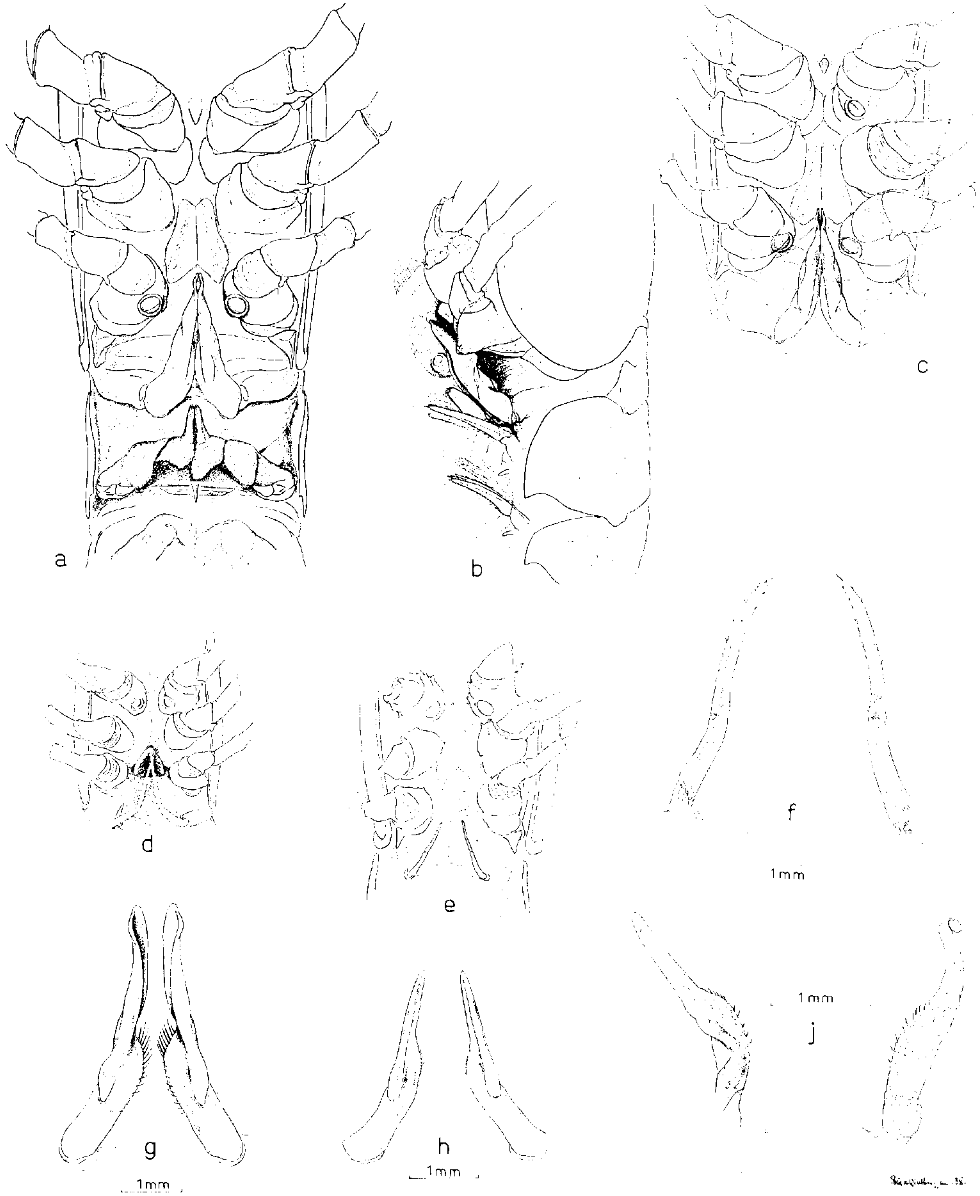
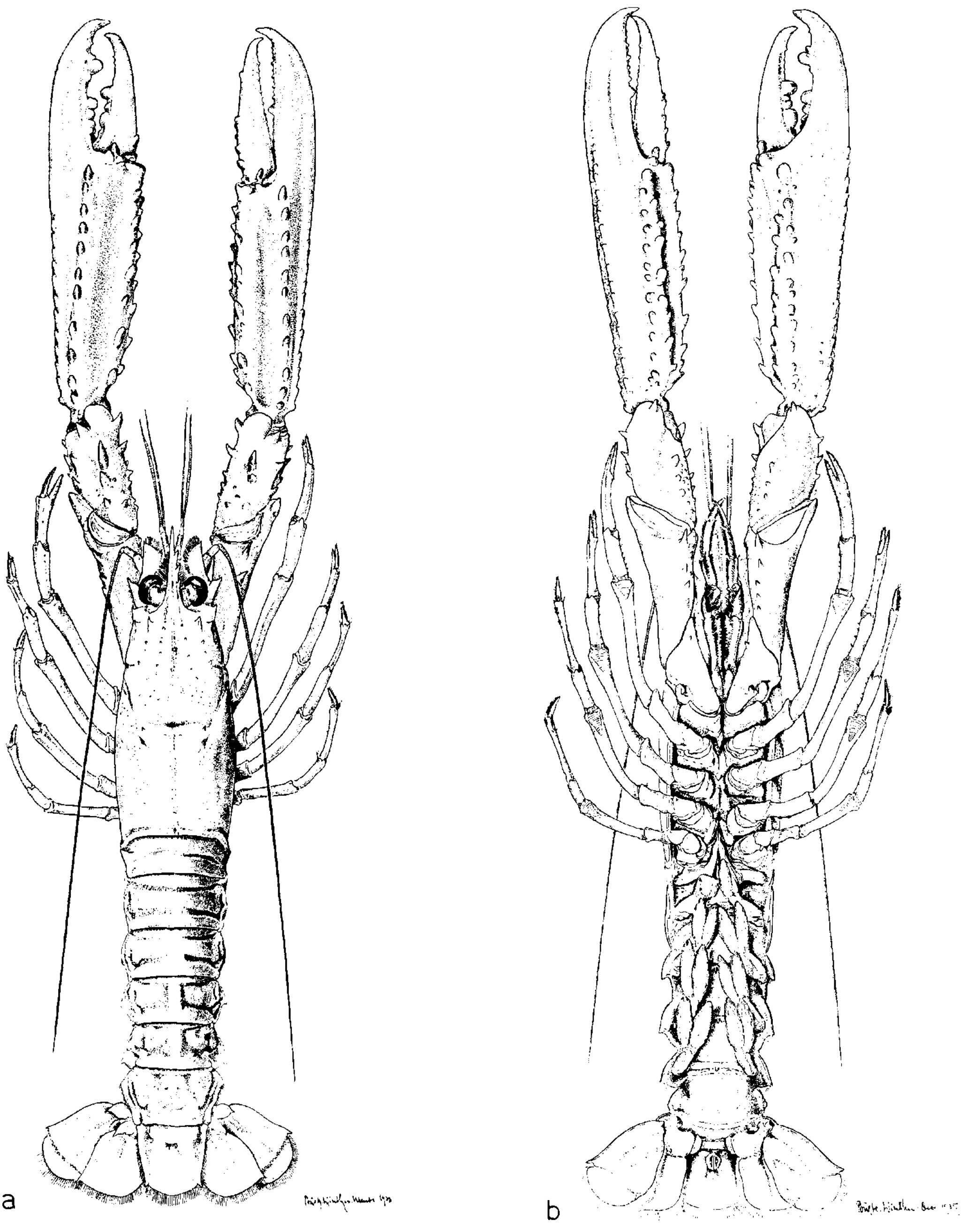


Plate VI. *Nephrops norvegicus* (L.) from Faeroe Waters. Total view.

a. Male of 23.3 cm total length (not counting hairs on telson). Dorsal view.
b. Same specimen as Plate VI a. Ventral view.

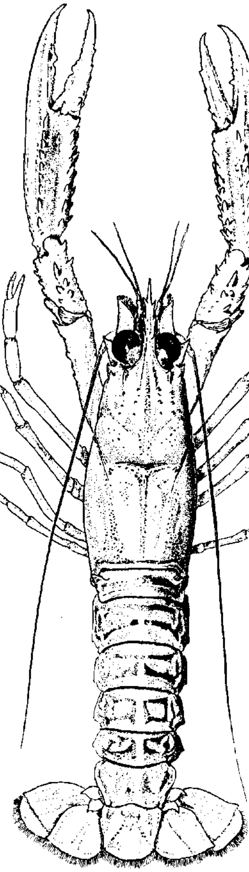
PLATE VI



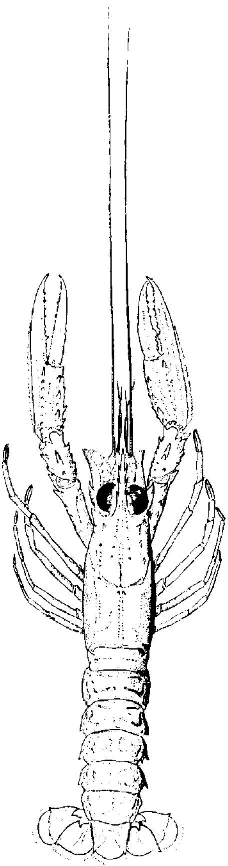
a b

Plate VII. *Nephrops norvegicus* (L.) from Faeroe Waters. Total view.

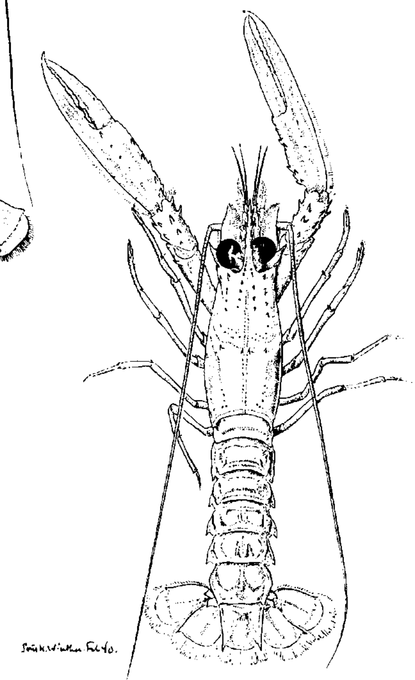
a. Female of 17.7 cm total length (not counting hairs on telson; total length including setae on telson: 18.1 cm; length including chelae: 25.9 cm). Dorsal view.
b. Female of 61 mm total length. Note the hairs on the claws.
c. Male of 48 mm total length (same specimen as Plate V h). Note the hairs on the claws.



a



b



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