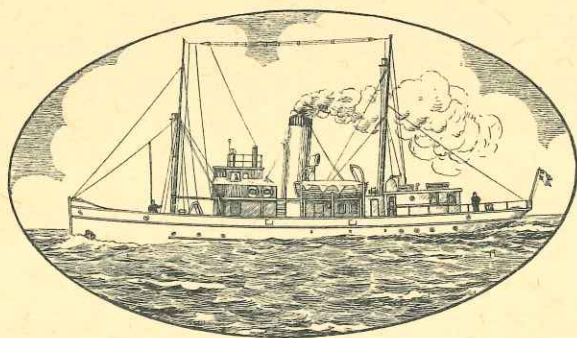


Report  
of  
The Danish Biological Station

to  
The Ministry of Fisheries



No. 53

By

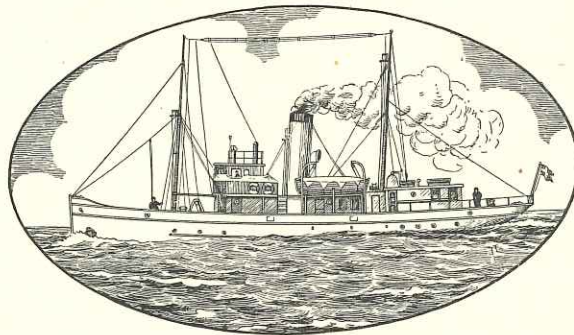
H. Blegvad, Ph. D.  
Director

Copenhagen · C. A. Reitzel

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## Fluctuations in the Amounts of Food Animals of the Bottom of the Limfjord in 1928–1950.

By H. BLEGVAD

THE Limfjord, which connects the North Sea with the Kattegat across the northern part of Jutland, is an ideal water for investigations on bottom animals. The fresh, salt water that flows through the fjord gives the bottom fauna good conditions of nourishment, and immediately outside the littoral zone the large, comparatively shallow broads in the western part of the fjord everywhere possess a soft

bottom, which is excellently suited for quantitative bottom sampling.

Regular investigations on the bottom fauna have now been carried out for nearly 40 years in this water with a special view to the animals that constitute the food of the fishes. Ever since C. G. JOHN PETERSEN in 1909 started his classical investigations with the bottom sampler the Danish Biological Sta-

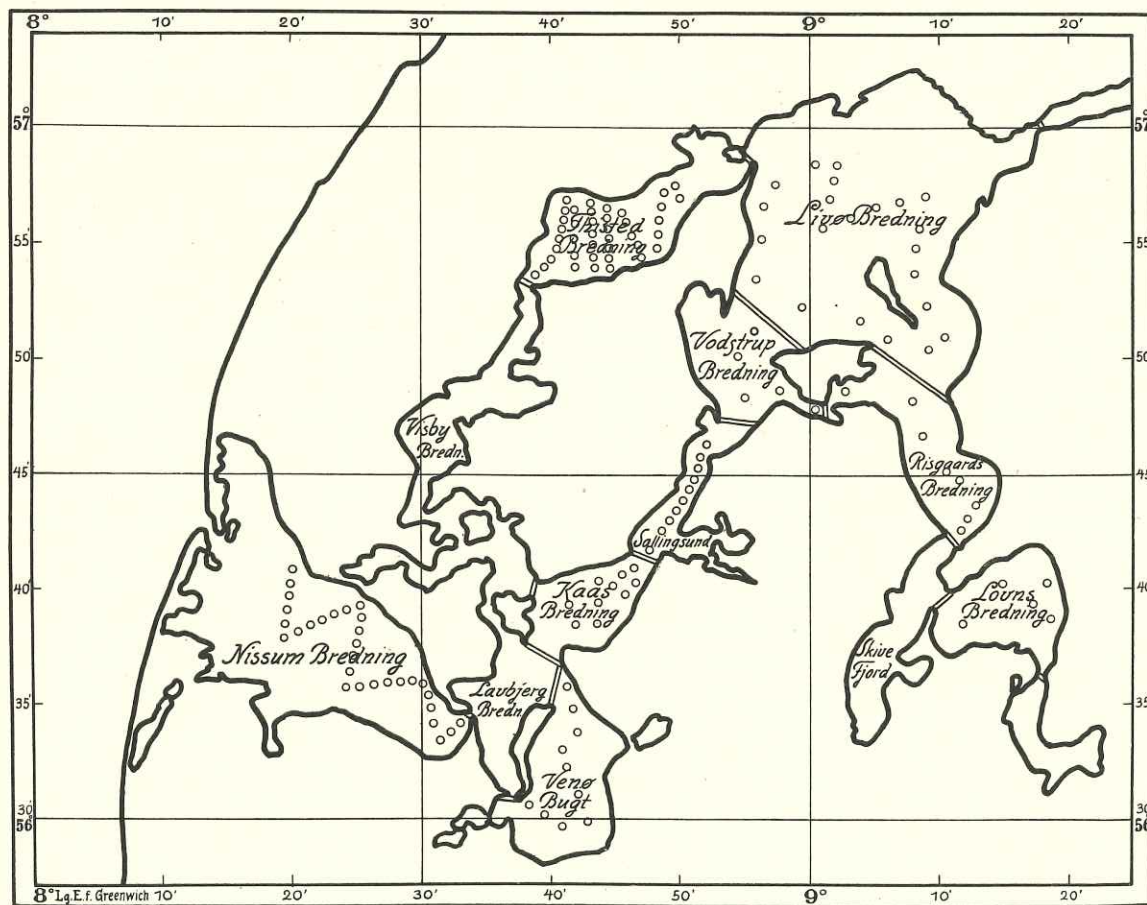


Fig. 1. Chart of the different Broads ("Bredning") of the Limfjord with the stations at which bottom samples were collected 1918–1950.

Kort over Limfjorden. Cirklerne viser, hvor der i årene 1918–1950 regelmæssigt er optaget bundprover.

tion every year has collected well over one hundred samples with the 0.1 sq.m. grab, and the animals found have been counted and weighed. Whenever possible investigations were carried out both in spring and autumn, and with the exception of quite a few years the station has managed to accomplish this program.

The investigations of 1909—17 were discussed by

like amphipods, *Cumaceae* and isopods, the gastropods *Philine aperta* and *Acera bullata* and all *Lamelli-branchia* not exceeding 3 cm. in length except *Corbula gibba* and *Nucula nitida* which are 2nd class fish food. The thick-shelled individuals of the genera *Mytilus*, *Pecten*, *Tapes*, *Cyprina* and *Mya* of more than 3 cm length are not taken by the fishes, but in their young stages they are 1st class food animals.

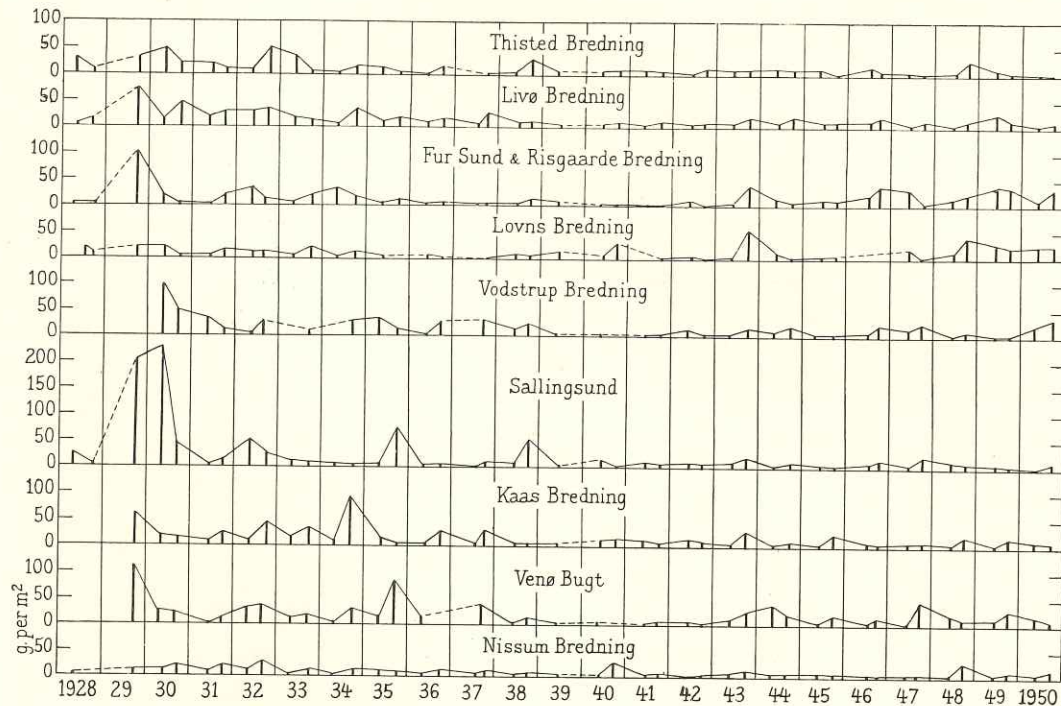


Fig. 2. Amounts of 1st class food animals in the different Broads of the Limfjord 1928—1950 expressed in grams (rough weight) pr. sq. metre.

Mængden af første classes fodedyr i de forskellige dele af Limfjorden udtrykt i gram råvægt pr. kvadratmeter i årene 1928—1950.

BOYSEN JENSEN (1919), those of 1918—27 by the present author (1925 and 1928). The last-mentioned paper contains a chart, reproduced here as Fig. 1, showing the stations at which the samples were collected; in all essentials this map also covers the years after 1928, so that a comparison can be made between results from before and after this point of time.

I have previously pointed out (1925) that the fishes exclusively or partially living on bottom animals, i. e. flat-fishes, eel, cod, viviparous blenny, etc., do not indiscriminately eat the animals found in the largest quantities on the sea bottom but prefer some species to others, which are taken only when no other food is available. As far as the Limfjord is concerned the former category—1st class food animals<sup>1)</sup>—include all polychaetes, all smaller *Crustacea*

In my discussion of the material from 1918—27 (1928) I made such a distinction between 1st and 2nd class food animals, expressed in grammes of rough weight per 1 sq.m.; in the following the results of the investigations of 1928—50 has been dealt with in the same way (Table 1). Fig. 1 in a graphical form shows the variations in the amounts of 1st class food animals during the same 23 years, so that they can be compared to the variations of the previous years, represented in fig. 1 of my paper from 1928.

<sup>1)</sup> Food animals in the present sense of the words are primarily those eaten by plaice inasmuch as the plaice is the most conspicuous bottom feeder of the Limfjord; but also the other species of fish mentioned here largely speaking live on the same bottom animals preferring the said 1st class food animals.

TABLE 1.

The amounts of 1st and 2nd class food animals in the different broads of the Limfjord in grammes of rough weight per 1 sq.m. of bottom.

		Thisted Broad.															
		Year... 1928		1929		1930		1931		1932		1933		1934		1935	
		Date... 15/4 18/9		21/9		14/5 2/9		14/6 26/9		1/5 26/9		5/4 29/9		23/4 23/9		10/5 24/9	
1st cl. food animals	<i>Abra alba</i> .....	16.6	2.2	12.7	28.0	3.8	0	0	0	20.4	6.8	0	0	5.2	6.5	0	
	<i>Solen pellucidus</i> .....	6.8	0.4	1.2	1.6	1.1	0.6	0.5	0.6	1.9	0.8	0.4	0.4	0.1	0.5	0.3	
	Other Molluscs .....	0.3	0.7	6.4	9.6	6.0	12.8	4.6	0.8	11.8	28.0	0.3	0.3	7.2	1.9	1.8	
	<i>Pectinaria koreni</i> ...	1.3	0.6	7.0	1.3	0.6	0	0.9	0.3	10.7	0.3	1.2	0	0.2	0.1	0.2	
	<i>Polychæta</i> .....	5.1	3.6	3.9	8.2	6.0	3.3	3.4	5.8	5.2	3.9	2.9	2.9	1.4	1.8	0.9	
Total...		30.1	7.5	31.2	48.7	17.5	16.7	9.4	7.5	50.0	39.8	4.9	3.6	14.1	10.7	3.1	
		Year... 1936		1937		1938		1939		1940		1941		1942		1943	
		Date... 26/5 21/9		22/9		13/6 16/9		7/6 23/5		6/9 19/6		24/9 10/6		23/9 1/6		19/9	
1st cl. food animals	<i>Abra alba</i> .....	0	1.4	0	0.4	0.5	0.1	0.3	0.2	0	0	0	4.7	2.8	0.7		
	<i>Solen pellucidus</i> .....	0	1.6	0.1	0.1	0.5	0.1	0.1	0	0	0.3	0.2	1.1	0.4	0.9		
	Other Molluscs .....	0.3	1.3	0.2	1.5	28.4	4.5	3.5	4.6	0.9	1.6	1.3	0.2	2.9	2.0		
	<i>Pectinaria koreni</i> ...	0	8.6	0.1	1.2	0.4	0.1	1.8	0.8	0.1	1.2	1.1	3.7	0.2	1.7		
	<i>Polychæta</i> .....	0.8	1.9	0.4	1.0	1.0	1.6	1.8	2.8	7.4	4.1	1.3	1.2	1.9	4.0		
Total...		1.1	14.8	0.8	4.2	30.6	6.4	7.5	8.4	8.4	7.2	3.9	10.9	8.2	9.3		
		Year... 1944		1945		1946		1947		1948		1949		1950		Average for 23 years	
		Date... 16/5 17/9		7/6 25/9		20/7 16/9		12/6 21/9		18/6 20/9		23/6 21/9		21/5 18/9			
1st cl. food animals	<i>Abra alba</i> .....	0.2	0	0	0.1	6.7	1.3	2.7	0	2.9	13.5	0.9	0	0	3.3		
	<i>Solen pellucidus</i> .....	0.6	0.1	0	0.1	0.6	0.2	0	0.1	0	0.1	0	0.1	0	0.6		
	Other Molluscs .....	3.5	2.2	5.9	0.1	1.3	0.2	0.6	0.1	0.4	5.3	3.8	0	0	3.9		
	<i>Pectinaria koreni</i> ...	3.2	0.6	0.3	0.6	1.6	2.0	0.9	0.3	0.8	7.5	3.6	0.1	0	1.6		
	<i>Polychæta</i> .....	6.7	6.0	5.4	2.4	5.6	2.2	1.3	0.6	1.4	1.9	0.9	1.5	1.1	0.9	3.0	
Total...		14.2	8.9	11.6	3.3	15.8	5.9	5.5	1.1	5.5	28.3	9.2	1.7	1.1	0.9	12.4	
		Livø Broad.															
		Year... 1928		1929		1930		1931		1932		1933		1934		1935	
		Date... 19/4 22/9		24/9		12/5 30/8		15/6 28/9		2/5 25/9		3/4 16/9		16/4 24/9		9/5 22/9	
1st cl. food animals	<i>Abra alba + nitida</i> ..	0	0.3	57.7	2.3	21.4	0	0.4	0.2	0.5	0	0.1	0	0.8	0.1	0.8	
	<i>Solen pellucidus</i> .....	0	0.3	0.9	0.3	6.4	0.7	0.6	0.7	1.0	0.3	0.3	0.3	10.1	3.0	2.1	
	Other Molluscs .....	0.6	11.9	7.0	1.6	4.0	1.9	3.5	2.7	24.2	3.7	12.4	0.8	24.5	7.1	13.8	
	<i>Pectinaria koreni</i> ...	0.1	1.0	2.6	0.4	4.0	0	0.5	0.2	0.8	0	0.3	0.3	3.0	0.2	0.8	
	<i>Polychæta</i> .....	2.3	5.1	7.6	9.5	10.3	15.0	20.7	24.2	2.8	12.9	1.3	5.5	1.8	2.6	2.0	
Total...		3.0	18.6	75.8	14.1	46.0	17.5	25.7	27.9	29.2	16.9	14.3	6.9	40.1	12.8	19.4	
2nd cl. food animals	<i>Nucula nitida</i> .....	4.0	0.3	0.4	0.3	0.4	1.1	2.3	1.3	2.2	2.0	3.3	2.8	0.7	2.5	0.9	
	<i>Corbula gibba</i> .....	3.8	44.6	32.5	33.1	56.6	36.5	18.5	20.5	21.5	28.4	57.3	28.0	9.3	26.1	19.8	
	Total...	7.8	44.9	32.9	33.4	57.0	37.6	20.8	21.8	23.7	30.4	60.6	30.8	10.0	28.6	20.7	
		Year... 1936		1937		1938		1939		1940		1941		1942		1943	
		Date... 20/5 15/9		4/7 18/9		12/6 12/9		5/6 21/5		5/9 13/5		23/9 3/6		18/9 30/5		18/9	
1st cl. food animals	<i>Abra alba + nitida</i> ..	0	1.6	0	0.8	0.7	0.2	0.1	0.1	0.1	0.1	0	0.1	0	2.1	4.3	
	<i>Solen pellucidus</i> .....	1.1	0.7	0.3	2.7	0.7	0.4	0.3	0.6	0.8	0.5	1.0	1.8	0.7	0.3	0.3	
	Other Molluscs .....	2.8	6.5	1.5	16.0	3.4	2.9	0.5	1.3	2.1	0	0.9	0.8	2.4	0.4	3.1	
	<i>Pectinaria koreni</i> ...	0.2	3.1	0.1	2.2	1.0	1.4	0.2	0.2	0.9	0	4.5	0.6	2.4	0.7	5.4	
	<i>Polychæta</i> .....	4.4	4.8	1.7	5.4	3.3	6.1	2.7	3.9	4.5	3.0	4.9	2.2	2.8	5.3	5.8	
Total...		8.4	16.6	3.6	27.0	9.0	10.8	3.7	6.0	10.1	3.6	11.3	5.5	8.3	8.8	18.9	
2nd cl. food animals	<i>Nucula nitida</i> .....	1.9	2.3	1.7	2.9	2.5	1.6	0.7	0.4	0	0	0.4	0.1	0.3	0.4	0.2	
	<i>Corbula gibba</i> .....	11.8	16.3	24.8	9.9	15.8	12.3	5.0	0.5	0.1	0.4	1.8	1.5	15.0	8.5	22.8	
	Total...	13.7	18.6	26.5	12.8	18.3	13.9	5.7	0.9	0.1	0.4	2.2	1.6	15.3	8.9	23.0	

(continued next page)

Table 1 continued.

## Livø Broad.

		Year... Date...		1944		1945		1946		1947		1948		1949		1950		Average for 23 years
		11/5	13/9	1/6	21/9	21/7	13/9	11/6	17/9	11/6	14/9	19/6	19/9	23/5	23/9			
1st cl. food animals	<i>Abra alba + nitida</i> ...	0.1	0.2	0	0.2	2.4	1.1	0	0	1.4	3.5	13.2	0	0.2	1.6			2.7
	<i>Solen pellucidus</i> ....	0.6	0.3	0.9	0.7	0.4	0.1	0.1	0	0	0.6	0.6	1.2	0.2	0.9			1.0
	Other Molluscs.....	1.3	4.1	1.4	0.7	0.5	9.6	0.3	10.1	0.2	2.4	0.1	6.0	1.2	0.7			4.6
	<i>Pectinaria koreni</i> ...	0.8	7.3	0.5	0.1	0.7	1.9	0.5	0.6	0.1	3.6	5.8	0.7	0.2	0.6			1.4
	<i>Polychæta</i> .....	4.3	7.9	5.1	6.0	7.8	4.1	2.9	2.2	2.0	3.8	4.9	4.9	3.8	6.6			5.7
Total...		7.1	19.8	7.9	7.7	11.8	16.8	3.8	12.9	3.7	13.9	24.6	12.8	5.6	10.4			15.4
2nd cl. food animals	<i>Nucula nitida</i> .....	0	0.1	0.1	0.2	0	0	0	0	0.1	0	0	0.1	0.1	0			0.9
	<i>Corbula gibba</i> .....	11.5	17.3	10.9	9.0	19.7	28.2	15.0	34.0	5.3	2.4	0.1	0	0.4	0.1			16.7
	Total...	11.5	17.4	11.0	9.2	19.7	28.2	15.0	34.0	5.4	2.4	0.1	0.1	0.5	0.1			17.6

## Fur Sound — Risgaards Broad.

		Year... Date...		1928		1929		1930		1931		1932		1933		1934		1935	
		18/4	21/9	23/9	15/5	29/8	16/6	27/9	3/5	19/8	6/4	20/9	22/4	24/9	15/5	27/9			
1st cl. food animals	<i>Abra alba + nitida</i> ...	0.8	0	84.5	3.2	0.6	0	13.8	11.4	3.2	0.2	12.4	4.8	5.4	0	6.0			
	<i>Solen pellucidus</i> ....	0.4	0	0	0	0	0	0	0	0.2	0	2.2	4.2	5.0	1.2	0.8			
	Other Molluscs.....	0.8	0.2	2.3	2.4	1.0	0.6	2.6	0.4	1.8	1.0	1.6	0.2	2.6	0.2	0.6			
	<i>Pectinaria koreni</i> ...	0	0.2	12.0	5.4	0	0	0	0	0.2	0.6	0.4	2.2	2.2	0	0.4			
	<i>Polychæta</i> .....	0.4	2.6	4.0	6.2	2.2	3.2	2.6	20.4	5.0	6.8	4.4	23.4	3.2	2.4	3.6			
Total...		2.4	3.2	102.8	17.2	3.8	3.8	19.0	32.2	10.4	8.6	21.0	34.8	18.2	3.8	11.4			
2nd cl. food animals	<i>Nucula nitida</i> .....	0	0	0.2	0.8	0.4	0.4	0.4	1.4	0.4	0.4	3.0	0.6	2.6	2.2	2.4			
	<i>Corbula gibba</i> .....	2.8	12.2	35.2	26.0	16.6	18.0	17.6	18.2	25.0	2.8	112.6	24.0	49.4	45.0	13.0			
	Total...	2.8	12.2	35.4	26.8	17.0	18.4	18.0	19.6	25.4	3.2	115.6	24.6	52.0	47.2	15.4			
		Year... Date...		1936		1937		1938		1939		1940		1941		1942		1943	
		25/5	23/9	4/7	23/9	16/6	17/9	5/6	20/5	8/9	11/6	28/9	7/6	19/9	28/5	21/9			
1st cl. food animals	<i>Abra alba + nitida</i> ...	0	2.6	0	0	0.2	1.0	0	0	0.2	0	0	0	0	2.0	22.8			
	<i>Solen pellucidus</i> ....	0	1.4	0	0	0	0	2.0	0	1.4	0.6	0.4	0.6	0.4	0	0			
	Other Molluscs.....	0.2	0	0.2	0	0.6	9.0	2.2	0	0	0	0	0.6	0	0	1.0			
	<i>Pectinaria koreni</i> ...	0	0.4	0	0	4.6	0	0	3.0	0	0.4	0.2	5.4	0	0.6	5.0			
	<i>Polychæta</i> .....	1.2	0.8	1.2	0.8	0.2	2.6	5.2	1.6	2.2	1.4	1.4	4.0	1.4	3.8	12.4			
Total...		1.4	5.2	1.4	0.8	5.6	12.6	9.4	4.6	3.8	2.4	2.0	10.6	1.8	6.4	41.2			
2nd cl. food animals	<i>Nucula nitida</i> .....	0.8	3.4	0.4	3.8	1.0	3.4	0	0.6	0	0	0.4	0	0	0				
	<i>Corbula gibba</i> .....	9.4	10.4	21.0	15.6	30.6	108.0	20.2	6.0	0.6	0	1.8	0	4.0	4.0	4.0			
	Total...	10.2	13.8	21.4	19.4	31.6	111.4	20.2	6.6	0.6	0	1.8	0.4	4.0	4.0	4.0			
		Year... Date...		1944		1945		1946		1947		1948		1949		1950		Average for 23 years	
		17/5	19/9	4/6	26/9	31/7	20/9	9/6	23/9	20/6	21/9	24/6	26/9	13/5	21/9				
1st cl. food animals	<i>Abra alba + nitida</i> ...	5.8	0	0	0	8.2	17.0	17.0	0	13.0	9.8	10.8	0	0	26.8			6.4	
	<i>Solen pellucidus</i> ....	1.2	0.8	0.6	0.1	1.6	0	3.0	0	0	0.4	4.2	2.4	0	0.4			0.8	
	Other Molluscs.....	0.6	0.6	0	0	0	8.8	1.4	0.6	0	0	1.6	0	4.4	1.4			1.2	
	<i>Pectinaria koreni</i> ...	10.6	0.2	0.4	0	1.8	3.6	4.0	0	0	7.0	19.9	26.4	1.8	0.2			2.7	
	<i>Polychæta</i> .....	6.2	3.8	12.1	10.2	10.6	12.4	7.6	0.4	0.6	7.2	4.0	6.2	3.2	5.8			5.0	
Total...		15.4	5.4	13.1	10.3	22.2	40.8	33.0	1.0	13.6	24.4	40.5	35.0	9.4	34.6			16.1	
2nd cl. food animals	<i>Nucula nitida</i> .....	0	0	1.6	0	0.6	0	0	0.2	0	0	0.4	1.6	0.2	0.2			0.8	
	<i>Corbula gibba</i> .....	10.0	26.8	2.4	0	18.6	25.6	13.8	46.0	44.6	130.0	118.0	136.0	104.0	102.0			32.5	
	Total...	10.0	26.8	4.0	0	19.2	25.6	13.8	46.2	44.6	130.0	118.4	137.6	104.2	102.2			33.3	

## Lovns Broad

		Year...	1928	1929	1930	1931	1932	1933	1934							
		Date...	4/7	21/9	23/9	15/5	29/8	16/6	27/9	3/5	19/8	6/4	20/9	22/4	24/9	
1st cl. food animals	<i>Abra alba + nitida</i> ...		14.2	7.4	16.6	0	3.2	0	2.4	0.8	0.4	0	14.2	0	0	
	<i>Mya truncata</i> juv...		0	0	0	0	0.2	0	0	0	0	0	0	0	0	
	Other Molluscs.....		2.2	4.1	0	11.8	0.2	0.4	3.6	0	5.8	1.4	5.1	1.0	9.7	
	<i>Pectinaria koreni</i> ...		1.2	0	5.0	0.4	0	0	0	0	0	0	0	0.2	0	
	<i>Polychæta</i> .....		3.4	1.0	0	10.4	2.0	3.8	11.2	8.6	4.4	2.0	1.2	0.4	2.3	
Total...			21.0	12.5	21.6	22.6	5.6	4.2	17.2	9.4	10.6	3.4	20.5	1.6	12.0	
2nd cl. food animals	<i>Corbula gibba</i> .....		1.2	4.8	1.0	7.2	1.2	0.4	0.6	0	0	0.6	1.2	0	0.7	
	Total...			1.2	4.8	1.0	7.2	1.2	0.4	0.6	0	0	0.6	1.2	0	0.7
		Year...	1935	1936	1937	1938	1939	1940	1941	1942	1943					
		Date...	15/5	25/5	23/9	23/9	16/6	17/9	6/6	20/5	8/9	27/9	7/6	19/9	28/5	21/9
1st cl. food animals	<i>Abra alba + nitida</i> ...		0	0	0	0	0.2	1.8	0	0	5.2	0	0	0	42.8	
	<i>Mya truncata</i> juv...		0	0	0	0	0	0.6	0	0	0	0	0	0	0	
	Other Molluscs.....		1.6	2.0	0	0	7.6	2.0	3.8	3.8	1.8	0.4	1.0	0	0.6	
	<i>Pectinaria koreni</i> ...		0.6	2.6	0	0	0	0	0	0	21.2	0.8	2.0	0	9.0	
	<i>Polychæta</i> .....		0.6	1.2	1.4	0	0	1.0	11.6	1.8	1.0	0.4	1.6	1.6	3.0	5.6
Total...			2.8	5.8	1.4	0	7.8	5.4	15.4	5.6	29.2	1.6	4.6	1.6	3.0	58.0
2nd cl. food animals	<i>Corbula gibba</i> .....		0.4	0	1.2	0	2.2	27.6	6.4	6.4	0.4	0.6	0	0	0	0.8
	Total...			0.4	0	1.2	0	2.2	27.6	6.4	6.4	0.4	0.6	0	0	0
		Year...	1944	1945	1947	1948	1949	1950	Average for 23 years							
		Date...	17/5	19/9	4/6	26/9	10/6	9/8	20/6	21/9	25/6	26/9	14/5	23/9	23 years	
1st cl. food animals	<i>Abra alba + nitida</i> ...		2.8	0	0	0	1.8	1.4	3.0	14.8	0.2	0	0	1.6	3.5	
	<i>Mya truncata</i> juv...		0	0	0	0	0	0	0	0.6	0	0	0	0	0.4	
	Other Molluscs.....		2.4	1.8	0	0	2.6	0.6	0.2	0.6	0.4	0	0	1.6	2.1	
	<i>Pectinaria koreni</i> ...		4.8	0	0	0.4	12.0	0	0	7.0	0.2	0	0	0.4	1.7	
	<i>Polychæta</i> .....		3.4	2.6	5.8	7.4	0.8	1.2	8.2	18.8	26.2	20.8	24.2	20.8	5.7	
Total...			13.4	4.4	5.8	7.8	17.2	3.2	11.4	41.8	27.0	20.8	24.2	24.4	13.4	
2nd cl. food animals	<i>Corbula gibba</i> .....		0.4	1.0	0.4	1.6	4.6	2.0	4.0	23.4	78.0	21.0	11.2	0.2	5.5	
	Total...			0.4	1.0	0.4	1.6	4.6	2.0	4.0	23.4	78.0	21.0	11.2	0.2	5.5

## Vodstrup Broad.

		Year...	1930	1931	1932	1933	1934	1935	1936						
		Date...	11/5	30/8	14/6	24/9	2/5	17/8	16/9	23/9	14/5	26/9	26/5	21/9	
1st cl. food animals	<i>Abra alba + nitida</i> ...		73.6	34.6	0	2.6	1.0	1.6	0	14.2	28.0	0.2	0	0.2	
	<i>Solen pellucidus</i> ...		8.2	0	0.6	0	0.8	0.4	3.0	0.4	1.0	0.2	0.8	0.6	
	Other Molluscs.....		1.2	5.6	9.0	1.0	2.8	15.4	7.0	12.8	0	8.2	0.6	18.0	
	<i>Pectinaria koreni</i> ...		0.4	0.6	0	0	0	2.4	0	0	0	0.4	0	7.4	
	<i>Polychæta</i> .....		16.0	4.0	26.6	6.2	1.6	8.2	0.6	2.0	7.4	4.4	2.0	2.0	
Total...			99.4	44.8	36.2	9.8	6.2	28.0	10.6	29.4	36.4	13.4	3.4	28.2	
2nd cl. food animals	<i>Nucula nitida</i> .....		0.4	1.0	1.2	6.6	4.6	3.8	6.0	0.2	4.4	0.2	0.4	0.4	
	<i>Corbula gibba</i> .....		42.6	67.6	20.6	21.4	24.8	54.0	180.0	50.8	126.0	20.2	27.6	29.0	
Total...			43.0	68.6	21.8	28.0	29.4	57.8	186.0	51.0	130.4	20.4	28.0	29.4	
		Year...	1937	1938	1939	1940	1941	1942	1943	1944					
		Date...	18/9	13/6	12/9	10/6	27/5	13/6	25/9	2/6	18/9	25/5	15/9	10/5	12/9
1st cl. food animals	<i>Abra alba + nitida</i> ...		2.2	2.2	0	0	0	0	0	0	1.0	0.4	0.2	0.4	
	<i>Solen pellucidus</i> ...		2.4	1.8	0.4	0	0	0	0.8	0	0.6	0	0.2	0.6	0.2
	Other Molluscs.....		27.0	0.4	19.2	0.4	0	0	1.4	1.4	0.8	0	0.6	0.6	7.8
	<i>Pectinaria koreni</i> ...		2.8	0	0.4	0	0	0	0.2	0	0.4	0	0	0	0.4
	<i>Polychæta</i> .....		3.0	9.4	3.4	5.4	5.4	6.6	4.6	11.4	2.0	1.8	14.0	9.0	13.6
Total...			37.4	13.8	23.4	5.8	5.4	6.6	7.0	12.8	3.8	2.8	15.2	10.4	22.4
2nd cl. food animals	<i>Nucula nitida</i> .....		0	0	0.4	0	0.4	0	0	0	0	0	0	0.2	0.4
	<i>Corbula gibba</i> .....		0.2	0.8	11.8	47.2	0.4	0	0.6	0.2	0.6	6.0	34.4	20.8	42.4
Total...			0.2	0.8	12.2	47.2	0.8	0	0.6	0.2	0.6	6.0	34.4	21.0	42.8

(continued next page)



Table 1 continued.

## Vodstrup Broad.

	Year... Date...	1945		1946		1947		1948		1949		1950		Average for 21 years
		31/5	21/9	22/7	14/9	10/6	17/9	19/6	21/9	26/6	25/9	23/5	20/9	
1st cl. food animals	<i>Abra alba + nitida</i> ...	0	0	0	0	0	0.2	0	0	0	0	0	0	4.3
	<i>Solen pellucidus</i> ....	0	0.4	0	0	0	0	0.4	0	0	0	0	0	0.7
	Other Molluscs.....	0	0.6	0.4	11.6	0.2	23.6	0	3.4	0	0	0	32.6	5.8
	<i>Pectinaria koreni</i> ...	0	0	0.2	0	0.2	0	0.2	0	0	0	0	0	0.4
	<i>Polychæta</i> .....	4.3	3.8	7.4	9.4	10.8	1.2	1.2	3.8	1.8	0.8	18.6	0.8	6.3
Total...		4.3	4.8	8.0	21.0	11.2	25.0	1.8	7.2	1.8	0.8	18.6	34.0	17.5
2nd cl. food animals	<i>Nucula nitida</i> .....	0	0	0	0	0	0	0	0	0	0	0	0	0.8
	<i>Corbula gibba</i> .....	42.0	0	65.0	0	1.2	3.4	0.4	0.4	0	0	0	0	25.5
	Total...	42.0	0	65.0	0	1.2	3.4	0.4	0.4	0	0	0	0	26.3

## Sallingsund.

	Year... Date...	1928		1929		1930		1931		1932		1933		1934		1935	
		20/4	20/9	20/9	10/5	26/8	12/6	24/9	4/5	27/9	4/4	17/9	21/4	19/9	14/5	25/9	
1st cl. food animals	<i>Abra alba + nitida</i> ...	0	0.4	149.6	192.6	25.2	0	0.2	0.2	1.8	0	0.4	0	0	0	0.4	
	<i>Solen pellucidus</i> ....	0	0.8	6.0	1.0	1.4	0	0	0	3.6	1.4	0.4	0.8	2.2	1.4	5.2	
	Other Molluscs.....	0	0.2	10.8	2.0	1.2	0	1.2	0.4	9.7	1.6	0	1.0	0.4	0.4	34.0	
	<i>Pectinaria koreni</i> ...	0	0.8	31.0	16.4	1.6	0	0.6	0	4.0	0.6	2.8	1.0	0.4	0.4	34.0	
	<i>Polychæta</i> .....	26.2	2.2	9.2	17.0	15.6	3.6	11.6	53.0	4.8	7.2	2.6	2.6	0.4	0.6	1.7	
Total...		26.2	4.4	206.6	229.0	45.0	3.6	13.6	53.6	23.9	10.8	6.2	5.4	3.4	2.8	75.3	
2nd cl. food animals	<i>Nucula nitida</i> .....	1.4	0.4	2.0	1.2	0	4.2	6.4	3.4	5.0	4.4	13.4	5.8	1.4	2.8	3.0	
	<i>Corbula gibba</i> .....	227.0	286.0	128.0	16.0	25.6	30.6	47.2	22.0	148.0	77.0	174.8	49.0	1.2	340.0	96.0	
	Total...	228.4	286.4	130.0	17.2	25.6	34.8	53.6	25.4	153.0	81.4	188.2	54.8	2.6	342.8	99.0	
1st cl. food animals	Year... Date...	1936		1937		1938		1939		1940		1941		1942		1943	
		22/5	22/9	3/7	19/9	17/6	13/9	10/6	19/5	9/9	14/6	26/9	6/6	17/9	29/5	15/9	
	<i>Abra alba + nitida</i> ...	0.2	0	0	0	0.2	0.2	0.4	0	0.4	0	0	0	0	0.6	0.6	
	<i>Solen pellucidus</i> ....	1.4	0	0	1.2	0	0	0	0	0	0	0	0	0.4	0.6	1.4	
	Other Molluscs.....	0.4	0.4	0	0.4	0	0	0	0.6	0.4	0	0	0	0.8	3.6	4.6	
	<i>Pectinaria koreni</i> ...	0.4	0.4	0	0.4	0	0	0	0.6	0.4	0	0	0	0.8	0	2.0	
<i>Polychæta</i> .....	1.2	2.2	0.2	6.6	6.8	55.4	1.8	13.8	1.0	8.2	5.8	8.2	5.4	7.0	7.0		
Total...		3.6	3.0	0.2	8.6	7.0	55.6	2.2	15.0	2.2	8.2	5.8	8.2	7.4	11.8	15.6	
2nd cl. food animals	<i>Nucula nitida</i> .....	0	0.4	0.4	0	0	0	0	0	0	0	0	0	0	0	0.2	
	<i>Corbula gibba</i> .....	46.6	262.0	56.0	23.2	56.0	304.0	3.0	1.2	0	0	0	0	0.2	0.6	121.0	
	Total...	46.6	262.4	56.4	23.2	56.0	304.0	3.0	1.2	0	0	0	0	0.2	0.6	121.2	
1st cl. food animals	Year... Date...	1944		1945		1946		1947		1948		1949		1950		Average for 23 years	
		14/5	16/9	31/5	24/9	26/7	19/9	16/6	22/9	15/6	15/9	25/6	20/9	15/5	13/9		
	<i>Abra alba + nitida</i> ...	0.6	0.2	0.4	0.4	0.2	0.2	0.2	0	0	0	0.4	0	0	0	8.5	
	<i>Solen pellucidus</i> ....	0.4	0	0	0.4	0	0.2	0	0	0	0.4	0	0	0	2.0	0.7	
	Other Molluscs.....	0	0.2	0	0.4	0.4	4.6	1.6	20.4	0	0	0	0	0	9.0	2.5	
	<i>Pectinaria koreni</i> ...	0.2	3.0	0.4	0	0	0.2	0	1.6	0	0.2	0	0	0	0	2.4	
<i>Polychæta</i> .....	0	5.0	3.1	1.6	8.6	9.8	1.6	1.8	11.4	8.4	2.8	1.6	0.6	1.2	7.9		
Total...		1.2	8.4	3.9	2.8	9.2	15.0	3.4	23.8	11.4	9.0	3.2	1.6	0.6	12.2	22.0	
2nd cl. food animals	<i>Nucula nitida</i> .....	0.4	0.2	0.6	0.4	0	0	0	0	0.2	0	0	0	0	0	1.3	
	<i>Corbula gibba</i> .....	94.0	54.0	94.0	206.0	226.0	380.0	31.6	0	0.2	0.2	0	2.4	2.4	0.2	82.6	
	Total...	94.4	54.2	94.6	206.4	226.0	380.0	31.6	0	0.4	0.2	0	2.4	2.4	0.2	83.9	

## Kaas Broad.

		Year...	1929	1930		1931		1932		1933		1934		1935				
		Date...	20/9	10/5	26/8	12/6	24/9	4/5	27/9	4/4	17/9	21/4	19/9	14/5	26/9			
1st cl. food animals	<i>Abra alba + nitida</i> ...		25.6	5.8	4.6	0.1	3.9	0.5	16.6	1.6	0.8	0	49.0	6.4	0			
	<i>Solen pellucidus</i> ....		9.4	0.9	0.5	0	2.0	1.3	0.4	2.4	0.8	2.6	0.4	0	0			
	Other Molluscs.....		8.2	5.1	0.2	0.2	6.8	1.1	19.4	1.8	28.2	1.2	39.9	1.8	1.6			
	<i>Pectinaria koreni</i> ...		13.4	1.6	1.7	0.2	0.8	0	4.0	0	4.0	0	0	1.8	0.2			
	<i>Polychæta</i> .....		6.0	7.2	9.7	8.1	11.9	4.2	3.6	10.4	1.4	1.0	5.0	5.6	2.8			
Total...			62.6	20.6	16.5	8.6	25.4	7.1	44.0	16.2	35.2	4.8	94.3	15.6	4.6			
2nd cl. food animals	<i>Nucula nitida</i> .....		4.8	6.5	8.7	18.8	24.7	11.8	32.6	16.0	9.4	9.6	8.1	4.2	2.2			
	<i>Corbula gibba</i> .....		92.0	32.7	121.5	98.8	141.8	63.2	146.4	160.0	222.8	132.0	131.0	270.0	52.0			
Total...			96.8	39.2	130.2	117.6	166.5	75.0	179.0	176.0	232.2	141.6	139.1	274.2	54.2			
		Year...	1936		1937		1938		1939		1940		1941		1942		1943	
		Date...	22/5	22/9	3/7	19/9	15/6	13/9	10/6	19/5	12/9	16/6	26/9	6/6	17/9	27/5	17/9	
1st cl. food animals	<i>Abra alba + nitida</i> ...		0	0	0.2	0.6	0.2	0.1	0.7	0.1	0.6	0	0	0.4	0	1.8	0.1	
	<i>Solen pellucidus</i> ....		0.5	0.2	1.2	2.8	0	0	0.1	0	0	0	0	0.2	0	0.8		
	Other Molluscs.....		2.2	28.0	0	17.4	0	2.7	0.5	0	6.0	0	0.8	1.6	2.8	0	14.5	
	<i>Pectinaria koreni</i> ...		0	0.5	0	2.0	1.6	0.1	0	0	0	0	0	0	0	0	0.8	
	<i>Polychæta</i> .....		1.6	1.0	2.8	3.8	5.2	3.5	5.4	12.0	7.6	9.6	4.0	13.6	5.4	1.4	11.0	
Total...			4.3	29.7	4.2	26.6	7.0	6.4	6.7	12.1	14.2	9.6	4.8	15.6	8.4	3.2	27.2	
2nd cl. food animals	<i>Nucula nitida</i> .....		1.9	0.2	1.8	0	0.2	0.2	0.1	0	0	0	0	0	0	0	0	
	<i>Corbula gibba</i> .....		185.0	81.0	77.0	79.0	47.0	53.5	32.0	4.0	0	0	0	0	0.4	23.0		
Total...			186.9	81.2	78.8	79.0	47.2	53.7	32.1	4.0	0	0	0	0	0.4	23.0		
		Year...	1944		1945		1946		1947		1948		1949		1950		Average for 22 years	
		Date...	13/5	16/9	8/6	24/9	23/7	19/9	16/6	22/9	15/6	15/9	20/6	25/9	15/5	13/9		
1st cl. food animals	<i>Abra alba + nitida</i> ...		0.2	0.2	0.2	0.6	1.0	0.2	0.1	1.8	1.6	0.1	0.2	0	0.2	—	3.0	
	<i>Solen pellucidus</i> ....		0.2	0.6	0	0.8	0.3	0.3	0.2	0	0	0	0.4	0.1	0	0.7		
	Other Molluscs.....		0.4	3.4	0	8.0	1.7	2.4	0.1	2.5	0	5.2	0	6.8	2.2	5.5	5.5	
	<i>Pectinaria koreni</i> ...		0	2.2	0	0.2	0	0	0	1.2	0	0.1	0	0	0	0	0.9	
	<i>Polychæta</i> .....		2.8	4.4	2.8	14.6	5.6	3.6	7.5	1.6	2.8	12.0	3.2	9.9	6.5	1.8	5.8	
Total...			3.6	10.8	3.0	24.2	8.6	6.5	7.9	7.1	4.4	17.4	3.4	17.1	9.0	7.3	15.9	
2nd cl. food animals	<i>Nucula nitida</i> .....		0.2	0.4	0	0	0	0	0	0	0	0	0	0	0	0	3.9	
	<i>Corbula gibba</i> .....		8.0	40.4	2.0	40.0	55.0	41.8	1.0	0.2	1.2	0	0	1.4	11.6	1.0	58.3	
Total...			8.2	40.8	2.0	40.0	55.0	41.8	1.0	0.2	1.2	0	0	1.4	11.6	1.0	62.2	

## Venø Bay.

		Year...	1929	1930		1931		1932		1933		1934		1935	
		Date...	18/9	13/5	1/9	12/6	23/9	4/5	21/8	3/4	17/9	21/4	19/9	11/5	24/9
1st cl. food animals	<i>Abra alba + nitida</i> ...		101.6	14.0	2.4	0.2	0.3	3.2	6.0	2.0	0.2	0	11.3	0.4	40.6
	<i>Solen pellucidus</i> ....		2.2	2.5	1.5	0.1	1.4	0.4	1.0	1.2	0.6	0.4	1.1	0	6.4
	Other Molluscs.....		0.4	0.9	5.6	0.5	4.9	4.0	25.4	4.4	15.8	2.5	13.6	15.8	27.4
	<i>Pectinaria koreni</i> ...		2.0	0	0.5	0	0.4	0	0.4	0	0	0	0.2	0	0
	<i>Polychæta</i> .....		6.0	7.6	9.8	2.7	6.8	24.2	6.8	4.8	1.8	0.6	6.5	2.0	9.4
Total...			112.2	25.0	19.8	3.5	13.8	31.8	39.6	12.4	18.4	3.5	32.7	18.2	83.8
2nd cl. food animals	<i>Nucula nitida</i> .....		0.4	2.0	2.0	5.8	6.3	5.0	17.6	2.0	13.2	3.1	2.1	0	0.2
	<i>Corbula gibba</i> .....		39.0	49.2	31.7	22.4	68.5	18.4	40.4	151.0	119.2	43.9	32.0	23.0	18.2
Total...			39.4	51.2	33.7	28.2	74.8	23.4	58.0	153.0	132.4	47.0	34.1	23.0	18.4

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Table 1 continued.

		Venø Bay.															
Year...		1936	1937	1938		1939	1940	1941		1942		1943		1944			
Date...		22/5	19/9	14/6	15/9	8/6	18/5	16/6	21/9	5/6	16/9	27/5	17/9	13/5	16/9		
1st cl. food animals	<i>Abra alba + nitida</i> ...	1.3	0	0	0.2	0.7	0	0	0	0	0	11.0	14.8	0	0		
	<i>Solen pellucidus</i> ....	0.7	0.9	0.4	0.2	0.3	0	0	0.2	0	0	0	0.8	0	0		
	Other Molluscs.....	1.3	34.4	0.4	9.6	0.1	2.3	0.8	3.4	0.4	0	0.6	8.2	1.4	18.0		
	<i>Pectinaria koreni</i> ...	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>Polychæta</i> .....	14.8	5.0	1.4	5.0	1.9	9.4	3.4	6.0	6.8	1.2	3.6	4.4	39.6	5.4		
Total...		18.1	40.5	2.2	15.0	3.0	11.7	4.2	9.6	7.2	1.2	15.2	28.2	41.0	23.4		
2nd cl. food animals	<i>Nucula nitida</i> .....	0.1	0	0.4	0	0	0	0	0	0	0	0	0	0	0		
	<i>Corbula gibba</i> .....	7.0	10.1	53.2	3.2	9.9	4.0	0	0	0	0	0.4	18.0	1.6	7.0		
	Total...	7.1	10.1	53.6	3.2	9.9	4.0	0	0	0	0	0.4	18.0	1.6	7.0		
Year...		1945		1946		1947		1948		1949		1950		Average for 22 years			
Date...		8/6	24/9	23/7	17/9	15/6	18/9	14/6	15/9	21/6	24/9	15/5	14/9				
1st cl. food animals	<i>Abra alba + nitida</i> ...	0	0	0.2	0	0.2	0	0.5	0.1	2.7	11.5	0.1	0	5.8			
	<i>Solen pellucidus</i> ....	0.6	0	0	0	0	0	0	0.6	0.5	3.1	0.2	0.5	0.7			
	Other Molluscs.....	1.0	22.4	1.0	8.6	0.2	47.5	12.2	20.9	0.1	11.6	4.1	4.8	8.6			
	<i>Pectinaria koreni</i> ...	0	0	0	0	0	0	0	0.2	0.1	0.8	0	0	0.1			
	<i>Polychæta</i> .....	4.8	1.2	2.4	4.0	1.5	1.5	7.7	8.4	9.8	5.5	11.6	2.9	6.6			
Total...		6.4	23.6	3.6	12.6	1.9	49.0	20.4	12.2	13.2	32.5	16.0	8.2	21.8			
2nd cl. food animals	<i>Nucula nitida</i> .....	0	0	0	0	0	0	0	0	0.1	0	0	0	1.6			
	<i>Corbula gibba</i> .....	23.6	43.0	10.7	8.4	0.2	0.1	0	0	0.2	0.3	0.1	0.1	22.0			
	Total...	23.6	43.0	10.7	8.4	0.2	0.1	0	0	0.3	0.3	0.1	0.1	23.6			
Nissum Broad East.																	
Year...		1928	1929	1930		1931		1932		1933		1934		1935			
Date...		17/4	19/9	7/5	26/8	10/6	22/9	5/5	21/8	4/4	18/9	18/4	20-21/9	12/5	25/9		
1st cl. food animals	<i>Abra alba</i> .....	0.5	4.0	1.6	6.2	0.1	6.3	0.9	14.0	0.2	2.1	0.1	2.6	1.0	0.7		
	Other Molluscs.....	0.3	0.8	2.1	1.0	0.9	4.6	2.4	3.2	1.1	5.4	0.7	3.0	5.4	3.5		
	<i>Pectinaria koreni</i> ...	0	1.5	0.1	2.5	0.2	2.8	0	5.8	0.1	0.7	0.1	1.9	0	0.9		
	<i>Polychæta</i> .....	1.9	4.0	9.4	9.5	6.0	3.5	8.3	4.6	2.7	2.2	1.7	4.1	3.1	3.1		
	Total...	2.7	10.3	13.2	19.2	7.2	17.2	11.6	27.6	4.1	10.4	2.6	11.6	9.5	8.2		
2nd cl. food animals	<i>Nucula nitida</i> .....	31.7	25.0	35.2	30.3	33.2	49.5	57.2	71.2	39.4	73.9	32.3	19.1	15.8	11.8		
	<i>Corbula gibba</i> .....	88.8	96.7	80.7	225.0	190.0	245.9	213.5	289.5	109.6	295.2	146.0	170.0	155.0	114.0		
	Total...	120.5	121.7	115.9	255.3	223.2	295.4	270.7	360.7	149.0	369.1	178.3	189.1	170.8	125.8		
Year...		1936		1937		1938		1939		1940		1941		1942		1943	
Date...		23/5	19/9	3/7	20/9	17/6	14/9	9/6	17-18/5	15/9	17/6	22/9	4/6	22/9	26/5	16/9	
1st cl. food animals	<i>Abra alba</i> .....	0.6	0	0.6	0.4	0.1	0.2	0.5	0.2	7.8	0.8	0	0.1	1.1	3.6	5.5	
	Other Molluscs.....	0.7	1.4	0.2	6.3	0.4	2.2	0.2	0.5	3.0	0	0.4	0	0.5	0.3	3.1	
	<i>Pectinaria koreni</i> ...	0.2	6.1	0.1	1.6	0	0.8	0	0.3	6.4	0	0.6	0	0	0	0.1	
	<i>Polychæta</i> .....	3.5	4.0	4.3	1.8	1.6	2.1	4.2	2.9	9.0	2.1	3.4	1.2	1.1	3.3	4.6	
	Total...	5.0	11.5	5.2	10.1	2.1	5.3	4.9	3.9	26.2	2.9	4.4	1.3	2.7	7.2	13.3	
2nd cl. food animals	<i>Nucula nitida</i> .....	11.7	4.7	3.8	3.1	3.5	3.7	2.3	4.1	4.8	2.6	14.2	11.0	3.9	6.0	12.9	
	<i>Corbula gibba</i> .....	132.5	66.5	102.0	30.3	22.5	27.1	30.5	24.5	24.0	1.2	6.0	0.3	0.6	0.5	9.8	
	Total...	144.2	71.2	103.8	33.4	26.0	30.8	32.8	28.6	28.8	3.8	20.2	11.3	4.5	6.5	22.7	

## Nissum Broad East.

Year...		1944		1945		1946		1947		1948		1949		1950		Average for 23 years
Date...		12/5	14/9	2/6	23/9	24/7	18/9	13/6	2/8	12/6	16/9	20/6	22/9	16/5	14/9	
1st cl. food animals	<i>Abra alba</i> .....	0.4	0.5	1.5	1.2	0.8	1.0	0.1	0	1.2	0.9	0.7	0.3	0.2	0.1	1.6
	Other Molluscs.....	0.7	1.2	0.3	1.9	0.9	1.3	0.1	1.7	0	12.0	1.7	5.4	3.3	10.6	2.2
	<i>Pectinaria koreni</i> ...	0	0.3	0	2.3	2.4	1.0	0	0.3	0	1.0	0	0.8	0	1.4	1.0
	<i>Polychæta</i> .....	4.7	4.7	5.1	1.6	2.4	2.0	3.2	2.7	2.3	13.1	2.4	30.0	2.4	3.1	3.9
Total...		5.8	6.7	6.9	7.0	6.5	5.3	3.4	4.7	3.5	27.0	4.8	9.5	5.9	15.2	8.7
2nd food animals	<i>Nucula nitida</i> .....	1.3	2.7	4.0	3.2	4.5	1.4	1.0	0.0	0	0.01	0.1	0.5	0.6	1.5	14.9
	<i>Corbula gibba</i> .....	2.8	13.4	14.2	4.8	7.6	2.6	3.5	3.6	0.5	11.5	15.5	17.8	36.0	97.5	72.8
	Total...	4.1	16.1	18.2	8.0	12.1	4.0	4.5	3.60	0.5	11.6	15.6	18.3	36.6	99.0	87.7

If we want to know how important the amount of food animals is to the fish life of the Limfjord, it is necessary to find out how large the production of food animals has been per 1 unity of area and per year. P. BOYSEN JENSEN (1919) has tried to calculate the annual production and consumption of bottom animals of the Thisted broad in the years 1910—17 on the basis of the samples collected in spring and autumn, but he admits that so many errors are involved in these calculations, that a precise knowledge of the annual production cannot be gained in this way. The figures resulting from the collecting of bottom samples illustrate only the momentary stock of bottom animals at the given time, and we do not learn how many of this population are devoured by other animals or die from other causes in the course of the year. We are informed only of the quantity at the disposal of the fishes at the time in question, but if the feeding of the fishes does not reach such an extent that so to speak all 1st class food animals are kept down at a minimum like a lawn that is constantly being mown, which is the case in the Nissum broad, we generally find proofs of the occurrence of rich spawning years of different bottom animals. Several instances of this kind are mentioned in my paper from 1928.

If we compare fig. 2 of the present paper with fig. 1 of the 1928 paper, we will find that comparatively large amounts of 1st class food animals were found in several broads in the autumn of 1929. It will appear from table 1 that this is mainly due to the fact that the small white bivalve *Syndosmya* (*Abra*) *alba* had a very rich spat-fall in this year. Also the chaetopod *Pectinaria Koreni* was well represented in several localities. As late as the spring of 1930 two of the broads (Thisted and Sallingsund) still showed rich stocks of these animals, but other-

wise it will be seen that very few of all the other years show any considerable occurrence of young of food animals and not by far in so enormous quantities as those appearing in several of the years 1910—27. The broads at Thisted, Livø, Sallingsund, Kås and Venø bay, which are so important fishing waters of the Limfjord, show practically no instances of particularly rich year-classes of any of the food animals during the long period between 1933 and 1950. It is well-known that the usual inconsiderable amount of 1st class food animals in the Nissum broad is due to the overpopulation of plaice in this water, but it appears from table 1 that even the 2nd class food animals of this broad have decreased considerably in number during recent years.

What is the cause of this marked decrease in the amount of food animals? It would be an obvious conclusion to seek a connexion in the disappearance of the eel-grass (*Zostera marina*) in 1933, more especially because the decrease is particularly pronounced after this time and because C. G. JOH. PETERSEN and his collaborators emphasized the importance of this plant in the diet of the detritus-eating bottom animals. The eel-grass, however, is still found in many bays and creeks of the Limfjord, especially near outfalls of fresh water; furthermore, large quantities of algae still occur everywhere along the coasts of the Limfjord, and so there will hardly arise any lack of vegetable matter on the soft bottom in the open sea, where moreover an enormous amount of decaying vegetables has been settling for centuries.

It is more probable, as I emphasized in my paper from 1928, that changes in temperature will prove to be an important determining factor as regards the richness or paucity of the spawning years of the food animals in question. We know that severe ice-winters often kill large amounts of marine

bottom animals (H. BLEGVAD, 1929). In 1939/40, 1940/41 and 1941/42 we had three consecutive severe ice-winters, and it will appear from fig. 2 and table 1

of fish transplanted to the Thisted-Visby broads in the years 1908—27 and the surface temperature at Oddesund (the sound between the Nissum and Lav-

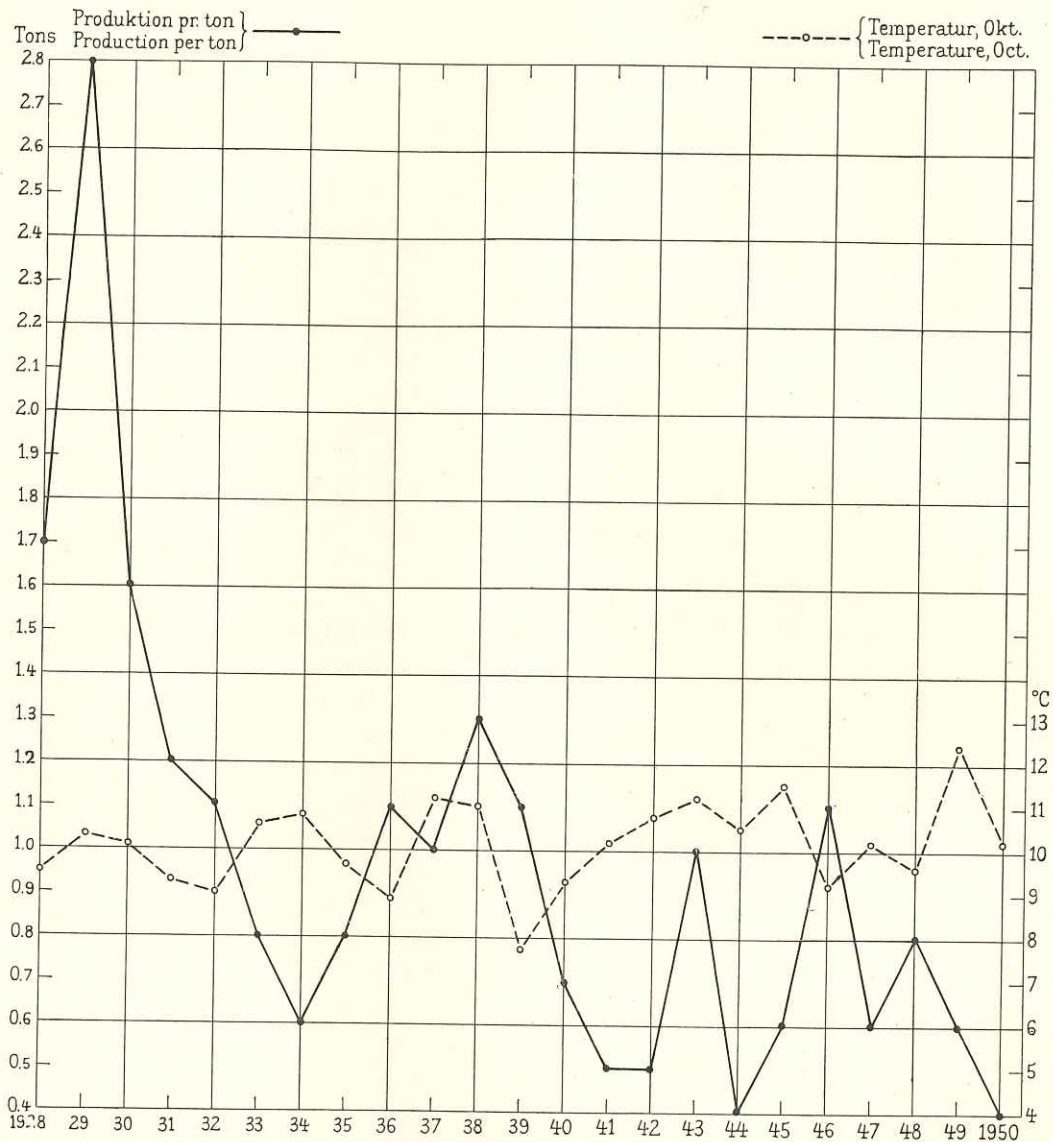


Fig. 3. Comparison between yield of the plaice fishery in Thisted-Visby Broads per ton of plaice transplanted to this region and the surface temperature at Oddesund in October during the years 1928—1950.

Sammenstilling af udbyttet af rødspættefiskeriet i Thisted-Visby Bredninger, beregnet pr. ton rødspætte omplantet til disse farvande, og den gennemsnitlige overfladetemperatur ved Oddesund i oktober måned i årene 1928—1950.

that all spring samples of 1940, 41 and 42 were extremely poor.

Assuming that the temperature of the water must be one of the factors that influence the upgrowth of the food animals of the plaice AAGE J. C. JENSEN in his paper from 1928 examines the correlation between the production of plaice per 1 metric ton

bjerg broads, i. e. at a considerable distance from the Thisted-Visby broads) in the months of August—November. He found a positive correlation between the production of plaice per 1 ton of transplanted fish and the temperature in October, but not in the other months (*l. c.* p. 97, fig. 3).

Fig. 3 gives the graphs for these two factors in

the years 1928—50. Even without a calculation of the coefficient it is easy to see that there is no positive correlation here. It is also apparent that the production of plaice per 1 ton of transplanted fish in the years after 1930 has decreased considerably, especially as compared to the period 1908—27 in Dr. JENSEN's fig. 3, although the temperatures of the later period on an average are somewhat higher than

Another factor, to which I have called attention in my 1928 paper, is the amount of viviparous blenny, which varies very much in the Limfjord. In fig. 2 of the said paper I have demonstrated that a large population of cod in the fjord coincides with a small population of viviparous blenny and *vice versa*, and I have advanced the hypothesis that the large quantities of viviparous blenny (and goby) in

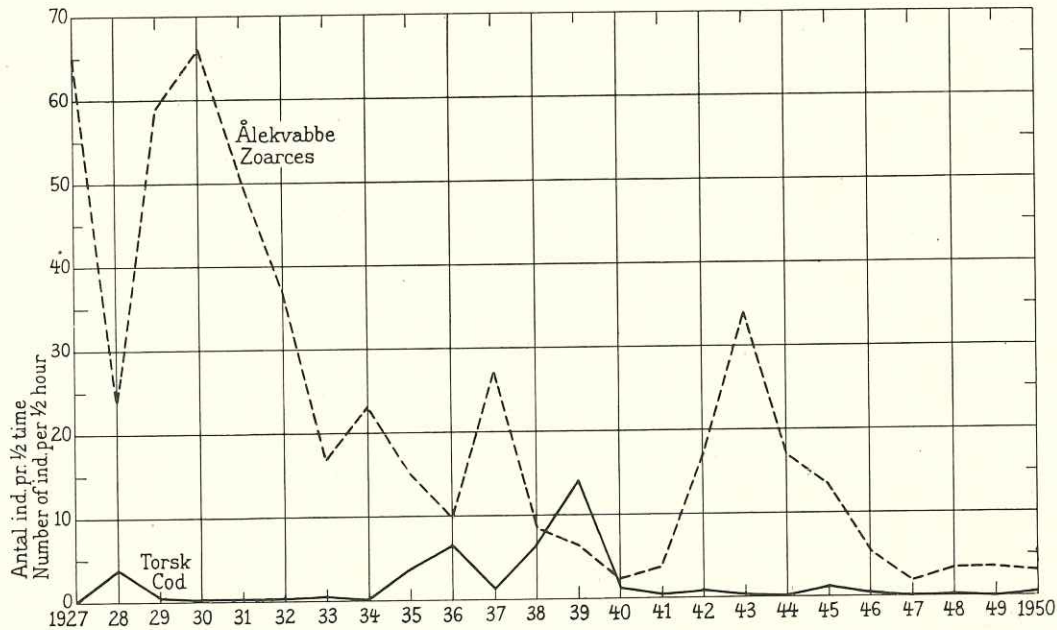


Fig. 4. Mean number of Cod and Zoarces caught per  $\frac{1}{2}$  hours fishing with eel-trawl in the Limfjord 1927—1950.

Gennemsnitlig antal torsk og ålekvabber fanget pr.  $\frac{1}{2}$  times træk med en finmasket åletrawl i Limfjorden i årene 1927—1950.

those of the latter. The very low production in 1940, 41 and 42 after the 3 severe ice-winters accords with the fact that the amounts of food animals as mentioned above were very small in these years. The largest production of plaice per 1 ton of transplanted fish occurred in 1929, which also corresponds with the fact that rich stock of food animals were found within vast areas of the Limfjord in this years. It may be added that according to the statistics the whole of the Limfjord yielded exceptionally rich catches of plaice in 1929.

We may accordingly state that although no absolute correspondence can be established between the available data of surface temperatures and the momentary stocks of food animals or plaice there is no doubt whatever that exceptionally anomalous conditions of temperature greatly influence the appearance of food animals.

the years 1924—27 through their considerable consumption of bottom animals are responsible for the very pronounced shortness of food animals in the Limfjord during these years.

In fig. 4 I have illustrated the results of the precision fisheries of the Biological Station for cod and viviparous blenny in the Limfjord during the years 1927—50. The graphs give the mean figures of each year for cod and viviparous blenny, respectively, caught per 30 minutes with a small-meshed trawl gear ("eel-trawl"). It will be seen that the stock of cod during all these years has been small as compared to the stock of viviparous blenny, and it may be added that the former mostly consisted of quite young individuals of the 0- and I-groups. As a matter of fact the cod fishery of all these years was insignificant, ranging between 46 and 346 tons per year. In spite of this the graphs of fig. 4 for several of

the years show a smaller stock of viviparous blenny when the cod population increases and *vice versa*. It will also be seen that the years 1940 and 41, after the severe ice-winters, showed comparatively small stocks of both viviparous blenny and cod. But the rapid fall of the stock of viviparous blenny during the years after 1943 cannot be explained from an increase of the cod population. Other factors must have been active here.

During the period considered here the output of the fishing of bottom fishes in the Limfjord does not show very great fluctuations, and it has not been possible to find any correlation between amounts of catches and food animals. But it should be emphasized that the fishing has been constantly intensified by the employment of gears of higher fishing capacity and by increased motor power. There is no doubt that the stocks of both eel, cod and plaice have decreased together with the amounts of food animals found per 1 unity of area.

The present writer some years ago had an opportunity to watch the effect of an oyster dredge hauled over a soft bottom with a rich population of bottom animals in the Limfjord, by walking in diving dress along the track made by the dredge. I was very much impressed to see how the star fish, the ophiurids, the crabs and the whelks hastened from both sides of the track to devour the tiny bottom animals: *Syndosmya*, *Solen*, *Nephtys* etc. who had been torn up from the bottom by the dredge and who were now lying on the surface of the bottom, many of them badly mutilated, as a helpless prey to the predatory animals. Even if it must be admitted that the dredge is specially designed to tear up the bottom, the modern otter trawls with their heavily weighted ground ropes will undoubtedly also stir up the soft sea bottom of the Limfjord and thus disturb the small food animals living there.

Originally the use of motor power for hauling the fishing gear was totally prohibited all over the Limfjord. In 1924 it was allowed to haul the Danish seine by mechanical force, and during the following years the fishing grew more and more intense. The legal length of the lines used by fishing with Danish seine was constantly enlarged (it is now 700 metres), and although the fishing of flat fish with otter trawl always has been—and is still—prohibited, a new gear was introduced in the Limfjord in the thirties: the eel trawl, an otter trawl of great efficiency when operated from boats with powerful motors. This gear

is now in general use all over the fjord and the motor power of the fishing boats has, as said above, constantly increased. It is, therefore, obvious that the sea bottom in the Limfjord, a limited area with an extremely soft bottom, during the later years has been ploughed up by trawls and other fishing-gears to a far higher degree than before. This fact must be taken into consideration too, as one of several possible causes of the marked decrease in the amount of food animals in the Limfjord during recent years.

### Concluding remarks.

The main results of the present investigations can be summarized in the facts that there have been only slight variations in the amount of food animals in the Limfjord during the period 1928—50, as compared with the preceding years, and that the amounts of 1st class food animals, as established by means of the bottom sampler, on an average were much lower for this period than the quantities found during the years 1909—27 (see H. BLEGVAD, 1928). Some degree of correspondence has been observed between periods of extreme cold and small quantities of food animals, but it is considered unlikely that the disappearance of the eel-grass from the Limfjord in 1933 should in any considerable degree be a contributory cause of the decrease in the amount of food animals.

It has been shown that the stock of viviparous blenny, which devours many bottom animals, was comparatively large during much of the period considered and that the cod population, which normally keeps down the numbers of viviparous blenny, at the same time was small. But during the said period no correspondence was found between the surface temperature in October and the production of plaice per 1 ton of fish transplanted to the Thisted-Visby broads (see AA. J. C. JENSEN, 1928).

No general correspondence could be established between the amounts of food animals and the yields of fishery, but the year 1929, which as mentioned showed the richest occurrence of food animals within the period of years considered, also yielded exceptionally heavy catches of plaice throughout the Limfjord.

During recent years the appearance of new fry of the food animals on one side and their mortality, including the consumption by the fishes, on the other seem to have been rather evenly balanced. Therefore the fluctuations in the amounts of food animals have

not been so great as in previous years when some year-classes were so rich that the fishes and other rapacious animals of the sea floor could not by far eat them up.

It is supposed that the stocks of bttom fishes (plaice, cod and eel) in the Limfjord have decreased simultaneously with the amounts of food animals found per 1 sq.m. of the sea floor. Based upon the authors' own experiences in diving dress it is emphasized that the increased use of trawls in the Limfjord may have had a detrimental effect upon the bottom fauna; this may be one of the reasons for the marked decrease in the amount of food animals during recent years.

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## Dansk Resum.

### Svingninger i mngden af fiskefde p havbunden i Limfjorden i rene 1928—1950.

Limfjorden er srlig egnet for undersgelser af mngden af fiskefde p havbunden; de forholdsvis lave dybder og den blde bund gr arbejdet med optagelsen af bundprver forholdsvis let. Biologisk Station har derfor lige siden 1909, med ganske f undtagelser, gennemfrt svel en forrs- som en efterrsundersgelse i Limfjorden hvert r, idet der p over hundrede forskellige steder optoges bundprver, og de fundne bunddyr blev talt og vejjet (fig. 1).

De fisk, der helt eller delvis lever af bunddyr, er frst og fremmest alle fladfiskene, dernst l, torsk, lekvabber, ulke og kutlinger. Men fiskene spiser ikke alt i flng, de foretrkker visse arter af bunddyrene for andre. De mest eftertragtede, »frste klasses fdedyr« er sm, tyndskallede muslinger og snegle, alle slags brsteorme og mindre krebsdyr. Til »anden klasses fdedyr«, der kun spises, nr intet andet kan fs, hrer visse arter sm, tykskallede muslinger, f. eks. de skaldte »hampefr«. De store, tykskallede muslinger som blmuslinger, sandmuslinger, kammuslinger og molbsters p over 3 cm's lngde spises slet ikke af fiskene; ungdomsstadierne er derimod frste klasses fdedyr.

Undersgelserne i rene 1909—27 er beskrevet af P. BOYSEN JENSEN og nrvrende forfatter. Her er behandlet undersgelserne i rene 1928—50. I tabel 1 er mngden af 1. og 2. kl. fdedyr (opgjrt i g pr. m<sup>2</sup> bundflade) i de forskellige Limfjordsbredninger gennem alle rene sammenstillet, og i fig. 2 er tallene for 1. kl. fdedyr fremstillet grafisk, s man fr over-

blik over variationerne i de forskellige Limfjordsbredninger fra forr til efterr og fra r til r.

I Nissum Bredning bevirker overbefolkningen af rdsptter, at bogstavelig talt alle 1. kl. fdedyr holdes nede p et minimum ligesom en grsplne, der bestandig klippes. I de vrige bredninger kan fiskene ikke spise s rent; i visse r, f. eks. efterret 1929, fandtes endog ret store mngder af 1. kl. fdedyr. Det skyldtes hovedsgelig, at den lille hvide musling *Abra alba* da havde et godt yngelr. Men sammenligner man fig. 2 med fig. 1 i min tidligere afhandling (1928) om fdemngden i rene 1918—27, vil man se, at der i alle rene efter 1929 kun er ganske enkelte, der viser en fdemngde af betydning, og at der slet ikke er tale om s store mngder som de, der fandtes i de tidligere r. Hvad er grunden til denne tilbagegang?

Som bekendt forsvandt legrsset fra Limfjorden i 1933 som flge af et sygdomsangreb. Dette kan dog nppe vre skyld i, at mngden af bunddyr er aftaget siden da; der er nemlig stadig store mngder af andre planter i Limfjorden, der kan danne grundlag for bunddyrenes ernring.

Mere sandsynligt er det, at srlig lave temperaturer kan virke drbende p bunddyrene. Sledes var der efter de tre strenge isvintre 1939/40, 40/41 og 41/42 usdvanligt f fdedyr tilbage. Derimod har det ikke vret muligt at finde overensstemmelse mellem vandtemperaturen ved Oddesund og mngden af rdsptter fanget i Thisted og Visby Bred-



ninger, beregnet pr. ton omplantet fisk, gennem årene 1928—50 (fig. 3). AAGE J. C. JENSEN fandt (1928) en sådan overensstemmelse, men kun for oktober måned, for årene 1908—27.

I en tidligere afhandling (1928) har jeg påvist, at en stor torskebestand i Limfjorden falder sammen med en ringe bestand af ålekvabber og kutlinger, og omvendt; ålekvabber og kutlinger er nemlig en vigtig føde for torsken. I samme afhandling er fremsat den hypotese, at den store mængde ålekvabber og kutlinger, der fandtes i Limfjorden i årene 1924—27, skulle have forført så mange af bundens fødedyr, at bundprøverne opviste usædvanligt få af dem i de pågældende år. Fig. 4 viser, hvor meget der gennemsnitlig er fanget af torsk og ålekvabber pr.  $\frac{1}{2}$  times træk ved Biologisk Stations præcisionsfiskeri med en finmasket åletrawl i Limfjorden i årene 1928—50. Man vil se, at torskebestanden i alle årene har været forholdsvis ringe; fangsterne bestod overvejende af unge torsk,  $\frac{1}{2}$ — $1\frac{1}{2}$  år gamle, men desuagtet viser kurverne for adskillige års vedkommende, at når der var flere torsk, var der færre ålekvabber, og omvendt. Derimod kan den stærkt aftagende bestand af ålekvabber i årene efter 1943 ikke forklares ved torskebestandens tiltagen; her må andre faktorer have spillet ind.

Det har ikke været muligt at påvise nogen almindelig overensstemmelse mellem svingningerne i mængden af fødedyr og udbyttet af fiskeriet. Det kunne næppe heller ventes, idet den fundne mængde fødedyr ikke er et udtryk for, hvad der året igennem har stået til rådighed for fiskene; en stor fiskebestand kan f. eks. gøre et sådant indhug på fødedyrene, at det, bundhenteren viser os, kun er små rester. Men hvor der ikke ligefrem er overbefolkning af rødspætter, kan et godt yngelår for et eller flere af fødedyrene som regel konstateres, idet fiskene ikke formår at spise op. Således 1929, hvor der, som nævnt, over hele Limfjorden fandtes en særlig stor bestand af fødedyr, og det er interessant at bemærke, at netop året 1929 gav et særlig godt rødspættefiskeri overalt i Limfjorden.

Som helhed har udbyttet af fiskeriet i Limfjorden i perioden 1928—50 ikke vist særlig store udsving. Men samtidig er fiskeriet bleven stadig mere intensivt, redskabernes fiskeevne er bleven forstærket og

kraften forøget; bestanden af ål, torsk og rødspætte er derfor sikkert i virkeligheden gået tilbage. På grundlag af egne iagttagelser i dykkerdragt i Limfjorden må det endvidere anses for sandsynligt, at mange små bunddyr omkommer og fortæres af rovdyr som snegle, kvabber og søstjerner, når de rodes op fra bunden af et svært belastet, slæbende fiskeredskab. Der tænkes her især på åleskovlvoddet, der indførtes i Limfjorden i 30'erne. Medens man i andre farvande ikke har kunnet konstatere nogen skadelig indvirkning af vodredskaberne på bunddyrene, er det ikke usandsynligt, at det kan være tilfældet i et så begrænset og særlig blødbundet område som Limfjorden.

Svaret på det ovenfor fremsatte spørgsmål må derfor blive, at der kan tænkes 3 muligheder som årsag til den forholdsvis ringe mængde fødedyr, der er konstateret i Limfjorden i de sidste 23 år, nemlig

1) særlig lave temperaturer, således de strenge isvintre.

2) Den store mængde ålekvabber og kutlinger, der fandtes i begyndelsen af 30'erne, kan have holdt mængden af fødedyr nede. Denne teori svækkes dog ved det faktum, at ålekvabbebestanden i årene efter 1943 gik stærkt tilbage.

3) Det intensive fiskeri med stedse forøget maskinkraft og indførelsen af åleskovlvoddet kan have bevirket, at de små fødedyr i havbunden har lidt skade ved den stadige overskrabning af bunden.

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hvortil der er henvist ovenfor.

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# Changes in the Frequency of Larger Bottom Invertebrates in the Limfjord in 1927–50.

By ERIK M. POULSEN

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### 1. Introduction.

THROUGH the extensive valuations carried out with the Petersen grab throughout the years by the Danish Biological Station we have gained a solid knowledge of the distribution and the changes in frequency of the smaller bottom invertebrates in the Limfjord<sup>1</sup>). However, the numbers of larger bottom invertebrates taken in the bottom sampler are so small, that the valuations do not give a very reliable picture of their occurrence and frequency. But through the material that has been collected during the eel-trawl fishings of the Danish Biological Station in the course of years it is possible to get an idea of the distribution and changing frequency of the larger bottom animals.

On account of their size and quantity these larger bottom animals (crabs, prawns, lobsters, star-fishes, larger bivalves and snails) play a prominent part in the household of the fjord and hence in the fishery. Several of them are fished extensively. In 1949 the yields of these fisheries in the fjord were:

	Metric tons	1,000 Dan. kr.
Lobster, <i>Homarus vulgaris</i> .....	12	109
Prawn, <i>Leander adspersus</i> .....	5	28
Mussel, <i>Mytilus edulis</i> .....	12,725	436
Star-fish, <i>Asterias rubens</i> .....	2,100	147
Total...	14,842	720

Besides these 2.4 mill. oysters were caught. Of fishes alone 4,466 tons or less than  $\frac{1}{3}$  of the catches

of bottom invertebrates were taken in 1949. The values of the catches show a different state of things: lobster, prawn, mussel and star-fish brought in only 720,000 Dan. kroner while the fishes fetched 5,137,000 kroner. If the 2.4 mill. oysters are included, however, the value of the bottom invertebrates amounts to nearly half the value of the fishes. It is worth noting that the value of the mussel fishery (436,000 kr.) is nearly as high as that of the herring fishery in the fjord (499,000 kr.) and that the value of the star-fish fishery (150,000 kr.) is more than three times the value of the cod fishery (41,000 kr.).

In other words the direct value of these species in the fishery is high and may well be compared to that of the principal species of fish. But indirectly, too, these species and the other bottom invertebrates of common occurrence play a prominent part in the fishery because in many ways they affect the lives of the food fishes to a considerable extent. Several of them are important food animals of the fishes (prawns and crabs of the cod, *Philine* of the eel). Others are typical noxious animals: star-fishes, whelks and crabs greatly incommode the net fishery and will even make the fishermen stop it for periods. To a higher or less degree, finally, they are all feeding competitors of the utility fishes or their food animals.

<sup>1</sup>) P. BOYSEN JENSEN: Valuation of the Limfjord. I. Studies on the Fish-Food, etc. Rep. Dan. Biol. Stat. 26, 1919.

H. BLEGVAD: Quantitative Investigations of Bottom Invertebrates in the Limfjord, etc. Rep. Dan. Biol. Stat. 34, 1928.

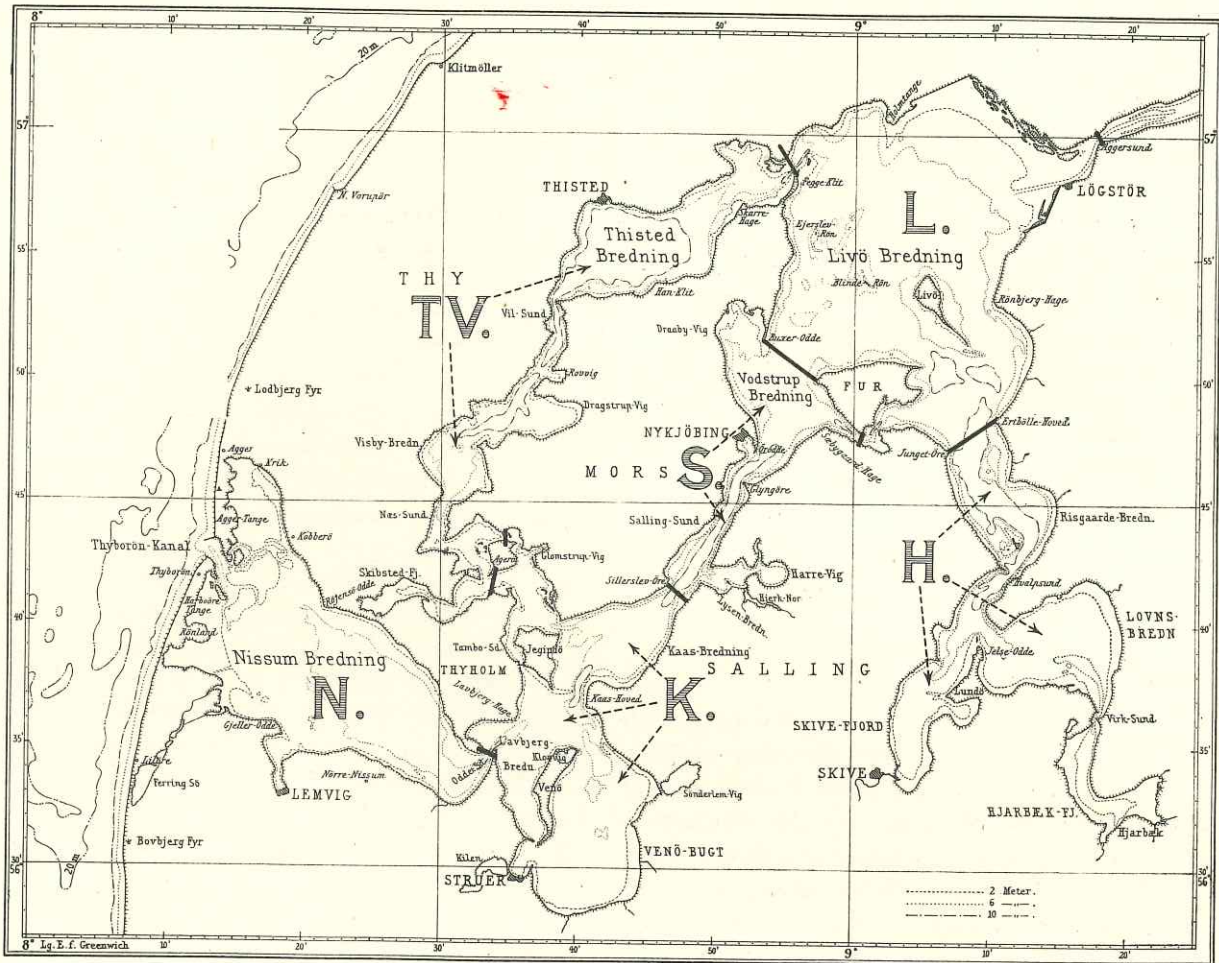


Fig. 1. Map showing the six regions (N—H) into which the Limfjord has been divided for working purposes.

Kort over den vestlige og mellemste del af Limfjorden visende grænserne mellem de 6 områder (N—H), hvori fjorden er opdelt.

From the view-point of the fishery there is accordingly any reason to give some attention to the larger bottom invertebrates, the more so because the Limfjord is a water of intense fishing, in which the species of fish need all the protection they can get. The development of a mussel and star-fish fishery will mean a certain protection of the hard pressed species of fish: during the time engaged in mussel and star-fish fishery a fishing boat not only spares the fish population, but it also helps it directly in keeping down its feeding competitors and noxious animals.

The various provisions for the advancement of the fishery, protection, transplantation and hatching, are based on an exact knowledge of the habits of the fishes and their conditions of life, and as feeding competitors and noxious animals the larger bottom invertebrates in fact constitute a factor that greatly affects the utility fishes in their conditions of living.

The bigger bottom invertebrates that will be dealt with here are:

1. *Metridium dianthus*, sea-anemone,
2. *Buccinum undatum*, whelk,
3. *Nassa reticulata*,
4. *Philine* sp.,
5. *Mytilus edulis*, mussel,
6. *Homarus vulgaris*, lobster,
7. *Leander adpersus*, prawn,
8. *Carcinus mænas*, shore crab,
9. *Portunus holsatus*, swimming crab,
10. — *depurator*, — ,
11. *Cancer pagurus*, edible crab,
12. *Hyas araneus*, spider crab,
13. *Stenorhynchus rostratus*,
14. *Eupagurus bernhardus*, hermit-crab,
15. *Crangon vulgaris*, shrimp,
16. *Asterias rubens*, star-fish,
17. *Ophiura texturata*, brittle-star,
18. *Psammechinus miliaris*, small sea urchin,
19. *Ascidia adpersa*, "sea squirt".

The material was collected with the eel-seine, a small-meshed trawl (lobsters and prawns are taken in small numbers only in the eel-seine, and so they are principally treated on the basis of the fishery statistics). The smallest mesh-size, in the bag, of the eel-seine is 14 mm (from knot to knot), and most animals down to a size of about 2 cm are retained. The results from the eel-seine are not nearly so exact as from the bottom sampler, partly because it is difficult to calculate the area covered by the former gear, partly because it does not take everything within the area passed over by the gear. In cases when there were many individuals or much bottom material the numbers of the different species were not counted but only estimated (10 — 20 — 50 — 100 individuals).

The eel-seine fishings were carried out in the western and central part of the fjord (Thyborøn to Løgstør) and twice a year, in May-June and in September of the years 1927—50; in the autumn of 1939 no investigations were made.

During the years 1927—50 certain changes have

In another respect this period has caused a change of conditions—though it is only a temporary one. The years 1940—42 brought 3 very severe ice-winters on end, a fact that is not known to have occurred before. For long periods the fjord was covered with ice, and the temperature of the bottom water was below 0° C. To many marine animals the cold and the ice-cover bring an intense aggravation of conditions and often cause a heavy mortality<sup>2)</sup>. In chapter 3 the influence of these changes of condition on the stock of bottom animals will be accounted for as far as the material allows.

## 2. Distribution and frequency of the species.

The part of the fjord covered by the investigation is divided into 6 areas (see the map fig. 1). N covers the Nissum Bredning (Broad), K the Lavbjerg Br. + Venø Bugt (Bay) + Kås Br., S the Sallingsund + Vodstrup Br., L the Livø Br., TV the Thisted Br. + Vilsund + Visby Br. and H Risgårde Br. + Hvalpsund + Lovns Br. + Skive Fjord.

TABLE 1.

Catch per  $\frac{1}{2}$  hour in eel-trawl of the various species in the different regions (means for the period 1927—50).

Area...		N	K	S	L	TV	H
<i>Metridium dianthus</i> .....	no. of ind.	5.3	9.1	20	12	19	9.5
<i>Buccinum undatum</i> .....	—	12	14	13	8.9	6.6	5.4
<i>Nassa reticulata</i> .....	—	15	18	10	5.2	5.1	3.9
<i>Philine aperta</i> .....	—	0.2	42	108	10	4.3	6.9
<i>Mytilus edulis</i> .....	litres	2.5	36	30	29	69	51
<i>Carcinus mænas</i> .....	no. of ind.	12	27	22	8.6	13	23
<i>Portunus holsatus</i> .....	—	4.1	0.4	0.1	0	0	0
<i>Portunus depurator</i> .....	—	2.1	0.1	0.03	0	0	0
<i>Cancer pagurus</i> .....	—	0.2	0.03	0	0	0	0
<i>Hyas araneus</i> .....	—	0.6	0.03	0	0.01	0	0
<i>Stenorhynchus rostratus</i> .....	—	3.3	5.1	10	5.8	16	5.8
<i>Eupagurus bernhardus</i> .....	—	17	1.4	0.6	0.3	0.06	0
<i>Crangon vulgaris</i> .....	—	21	35	58	32	54	43
<i>Asterias rubens</i> .....	—	80	80	73	18	27	14
<i>Ophiura texturata</i> .....	—	84	155	270	100	121	98
<i>Psammechinus miliaris</i> .....	—	6	21	25	32	21	15
<i>Asciidiella aspersa</i> .....	litres	18	13	19	5.8	9.0	2.2
Surface water salinity...	ca.	31 ‰	29	27—29	23—28	23—26	20—27

taken place in the conditions of the bottom animals in the Limfjord. In 1933<sup>1)</sup> the eel-grass disappeared from the greater part of the fjord; after this time it has appeared only in small patches of thin growth.

<sup>1)</sup> H. BLEGVAD: An Epidemic Disease of the Eel-Grass (*Zostera marina*). Rep. Dan. Biol. Stat. 39, 1935.

For the individual areas table 1 gives the mean catches of the different species per 30 minutes in the

<sup>2)</sup> A. C. JOHANSEN: Mortality among Porpoises, Fish and the Larger Crustaceans in the Waters around Denmark in Severe Winters. Rep. Dan. Biol. Stat. 35, 1929.

H. BLEGVAD: Mortality among Animals of the Littoral Region in Ice Winters. Ibid. 1929.

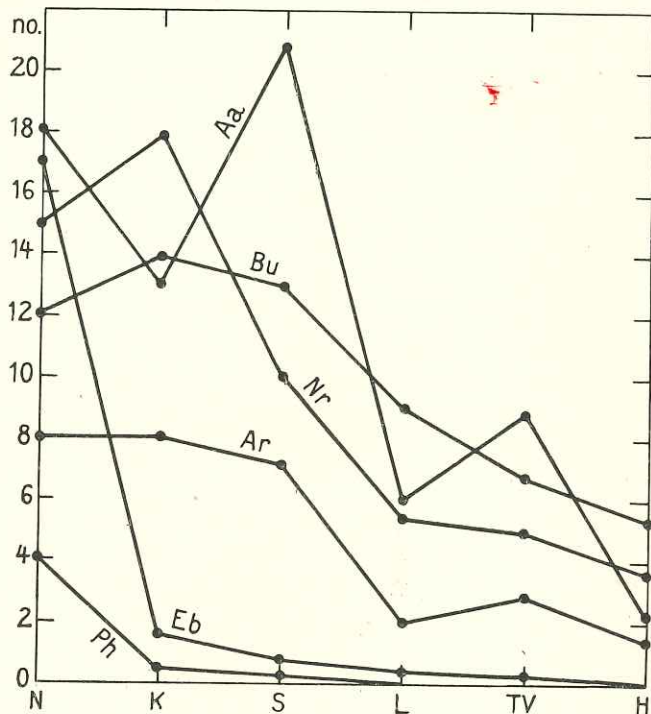


Fig. 2a. Species decreasing in number in an inward direction through the fjord.

Aa = *Asciidiella aspersa* (litres), Bu = *Buccinum undatum*, Nr = *Nassa reticulata*, Ar = *Asterias rubens*, Eb = *Eupagurus bernhardus*, Ph = *Portunus holsatus*.

Figurens kurver viser, hvorledes en række arter aftager i mængde ind gennem fjorden fra område til område (N—H, se fig. 1); tallene til venstre angiver antal individer, for søpung antal liter, taget i åletog pr. ½ time i middel for årene 1927—1950.

Aa = *Asciidiella aspersa*, søpung. Bu = *Buccinum undatum*, konksnegl. Nr = *Nassa reticulata*, dværgkonk. Ar = *Asterias rubens*, korsflsk. Eb = *Eupagurus bernhardus*, eremitkræbs. Ph = *Portunus holsatus*, svømmekrabbe.

eel-seine for the whole period 1927—50. The bottom row of the table states the approximate salinities of the surface water according to AAGE J. C. JENSEN<sup>1</sup>). As the fjord is very shallow, the difference in salinity between bottom and surface is small (about 0—0.5 per mille<sup>2</sup>).

It appears from the frequency figures of the table that the species broadly speaking fall into two groups (fig. 2a and b): one group, the species of which decrease in frequency from west to east, and another group with a comparatively uniform occurrence throughout the area examined.

To the first group—frequency decreasing from west to east—belong:

<sup>1</sup> AAGE J. C. JENSEN: Remarks on the Hydrography of the Limfjord. Rep. Dan. Biol. Stat. 34, 1928.

<sup>2</sup> ERIK M. POULSEN: Om Limfjordens Torskebestand. Skr. udg. af Komm. f. Danmarks Fiskeri- og Havunders. 11, 1942.

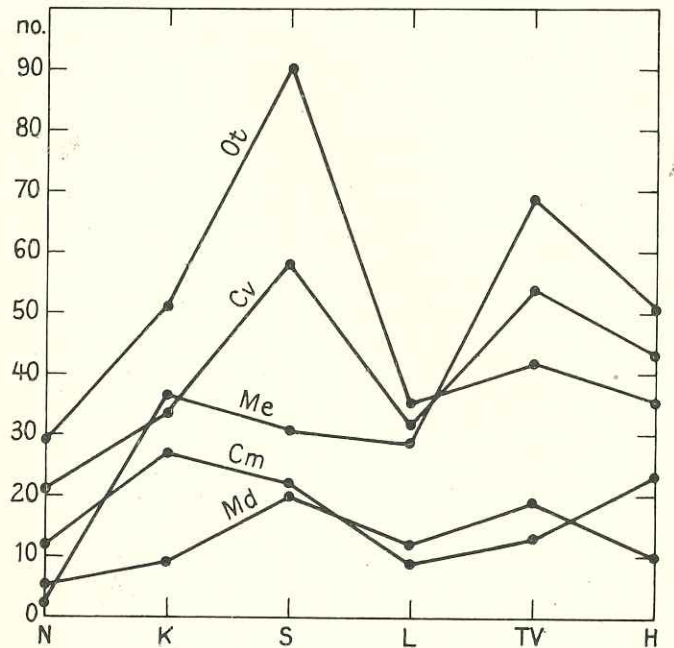


Fig. 2b. Species occurring in approximately the same numbers within all areas.

Ot = *Ophiura texturata*, Cv = *Crangon vulgaris*, Me = *Mytilus edulis* (litres), Cm = *Carcinus maenas*, Md = *Metridium dianthus*.

Kurver over hyppigheder af en række arter, der forekommer i nogenlunde samme mængde i fjordens forskellige områder (N—H, se fig. 1); tallene til venstre angiver antal individer, for blåmusling antal liter, taget pr. ½ time i åletog i middel for årene 1927—1950.

Ot = *Ophiura texturata*, slangestjerne. Cv = *Crangon vulgaris*, hestereje. Me = *Mytilus edulis*, blåmusling. Cm = *Carcinus maenas*, strandkrabbe. Md = *Metridium dianthus*, soanemone.

*Buccinum undatum*  
*Nassa reticulata*  
*Homarus vulgaris*  
*Portunus holsatus* and *depurator*  
*Cancer pagurus*  
*Hyas araneus*  
*Eupagurus bernhardus*  
*Asterias rubens*  
*Asciidiella aspersa*

There is hardly any doubt that the difference in frequency is caused by the decreasing salinity (in area N 31 per mille, in H 20—27 per mille): these species are not only rarer in the eastern area with the lowest salinity, but like the salinity their decrease in frequency from west to east is smooth. Also in the waters inside the Skaw the distribution of these species is determined by the decreasing salinity. In our inner waters the edible crab and the two swimming crabs, which in the Limfjord do not advance further than the Sallingsund, have their inner limits in the southern Kattegat. The lobster, which is still

found in the western part of Livø Br. and Thisted Br., has its inner limit in the Belt Sea. *Stenorhynchus rostratus*, which goes as far as Livø Br., and *Eupagurus bernhardus*, which also lives in Thisted Br., but does not advance E. of Salling (H), in our inner waters are found as far down as the western Baltic. Among the other species that occur in all 6 areas, although in rapidly decreasing numbers, *Buccinum undatum* and *Nassa reticulata* have their inner limits in the western Baltic, *Asterias rubens* in the area E. of Falstria, while *Ascidiella aspersa* only advances as far as the Sound.

To the second group—species that do not decrease in frequency through the fjord—belong:

*Crangon vulgaris*  
*Leander adspersus*  
*Carcinus mænas*  
*Mytilus edulis*

These species, accordingly, must be less sensitive—typically euryhaline—to lower salinities, which also appears from their distribution in the other Danish waters where they advance far into the Baltic.

The following species take up an intermediate position between these 2 groups:

*Metridium dianthus*  
*Psammechinus miliaris*  
*Ophiura texturata*  
*Philine* sp.

It is true that they are rarer in the eastern (H) than in the central areas, but they are also comparatively rare in the saltiest area (Nissum Br.). In their distribution they certainly depend on the salinity, but other conditions are involved causing the irregular decrease through the fjord in an inward direction. That they depend on the salinity, at any rate to some extent, appears from their distribution in the rest of our waters: in the Baltic none of them have been taken inside the water between Falstria and Rugen, while others do not enter the Baltic at all.

Within the area in which the salinity allows them to live the frequency of the species of course depends not only on the varying salinity, but also on a number of other conditions. In the two large and shallower broads, Nissum Br. and Livø Br., the bottom is comparatively hard, consisting of sand mixed with clay and covered only by a thin layer of ooze. In the other, mostly slightly deeper parts the bottom is softer, consisting mainly of mud and ooze. In their

frequency several of the species dealt with here show a distinct dependence on the nature of the bottom.

*Stenorhynchus rostratus*, which in Danish waters has its inner limit in the southern part of the Lesser Belt at a salinity of about 18 per mille, thus requires rather high salinities. In the different areas of the Limfjord it was taken in the following numbers per 30 minutes: N — 3.3, K — 5.1, S — 10.0, L — 5.8, TV — 16 and H — 5.8. In other words the smallest numbers occur in the saltiest region, and thus the salinity is only one of the conditional factors. The highest frequencies are reached in Sallingsund (S) and in Thisted-Visby Br. (TV), i. e. the areas in which the softest bottom occurs, the lowest frequencies in Livø and Nissum Br.s where the bottom is comparatively hard. In area K the comparatively hard bottom of Lavbjerg Br. gave only 2 individuals per 30 minutes while the somewhat softer bottom of Kås Br. and Venø B. yielded 8 individuals per 30 minutes. So it is evident that the frequency of this species in a high degree depends on the nature of the bottom. The fact, however, that the catch within the soft, muddy area east of Salling only amounted to 5.8 per 30 minutes no doubt means that the salinity of this region (20 per mille) is so low, that the quantity is kept down in spite of the excellent conditions offered by the bottom.

In the same way the snail *Philine* depends on the nature of the bottom. It is rare on the hard bottom of Nissum Br. (0.2 per 30 minutes) and most common on the soft bottom of Sallingsund (108 per 30 minutes). However, on the soft bottom of Thisted-Visby Br.s and E. of Salling the species again decreases in number (4.3 and 6.9 per 30 minutes). Here the lower salinity no doubt asserts itself, for this species is rather particular about the salinity: in Danish waters it does not advance further southwards than the westernmost part of the western Baltic.

The mussel occurs in large quantities, 29—69 litres per 30 minutes, in the whole central part of the fjord; it is rare, 2.5 l per 30 minutes, in Nissum Br. only. This great difference in frequency cannot be explained from the requirements of the species on salinity nor from the nature of the bottom because the possibilities of attachment would be as good in Nissum Br. as for instance in Livø Br. A possible explanation of the thin stock of mussels in Nissum Br., however, may be that the dense population of plaice (and dab) in the broad keeps down the mussels

by eating their youngs. Another possibility is that the current through the open parts of Nissum Br., to which the investigations were limited, is so strong that it prevents the spat from attaching.

Of two other species dealt with here and both belonging to the epi-fauna, i. e. adhering to other objects, *Ascidiella* shows a considerable decrease in an inward direction through the fjord while the sea-anemone (*Metridium*) shows a more irregular frequency. Their thriving depends on their finding objects to which they can attach themselves, stones, shells and the like. A comparison between the quantities of mussels and sea-anemones shows that on the whole many mussels are accompanied by many sea-anemones:

	N	K	S	L	TV	H
Mussels, litres . . . . .	2.5	36	30	29	69	51
Sea-anemones, numbers	5.3	9.1	20	12	19	9.5

A dense stock of mussels thus gives a dense stock of sea-anemones, apparently because the mussels constitute a good footing to the sea-anemones.

### 3. Changes in quantity from year to year.

Table 2 gives the mean numbers of individuals or litres for 3 years' periods between 1927 and 1950; the first period covers 4 years, the last one only 2 years<sup>1)</sup>. The figures represent the catches per 30 minutes, in means of the spring and autumn investigations for the year and area in question. The table further shows the total mean for each area. In calculating the total means only such areas were considered in which the species did occur.

There is an extremely pronounced variation of frequency from year to year. *Nassa reticulata* for instance in 1946—48 yielded only 1.1 individuals per 30 minutes against 20 ind.s per 30 minutes in 1931—33. The amounts of *Ascidiella* (measured in litres) ranges between 0.4 in 1937—39 and 43 in 1943—45. The poorest period of *Stenorhynchus rostratus* gave 1.2 ind.s per 30 minutes, the best period 17. These sudden changes in frequency from year to year are worth noting, not the less because it induces caution in the judging of faunistical or zoo-geographical results of investigations covering only shorter periods.

<sup>1)</sup> The arrangement was made in this way for the purpose of getting a separate period covering the 3 years with severe ice-winters, 1940—42.

The causes of these great fluctuations are manifold: cold in winter, temperature during the spawning period, conditions of nutrition, competition, etc. However, our knowledge of the biology and the changing conditions of the species is rather limited, and so the causes of the changes in frequency cannot be accounted for in detail. But the comparatively long period (24 years) in which investigations were carried out makes it worth while to give a statement of the changes and to try to find the principal or at least the most conspicuous causes.

#### a. The influence of the severe ice-winters on the frequency.

The first problem to be tackled here is the question whether the 3 severe ice-winters 1939/40, 1940/41 and 1941/42 have affected the frequency of the species. A look at table 2 will show that several species indeed have a frequency minimum in 1940—42. This is true of *Nassa reticulata*, *Philine*, *Psammochinus miliaris*, *Eupagurus bernhardus*, *Stenorhynchus rostratus*, *Portunus depurator* and *P. holsatus*.

In fig. 3 their frequencies are shown together with a graph indicating the mean temperature of the surface water in Oddesund in January-March. It is seen that the pronounced minimum of temperature in 1940—42 coincides with a minimum of frequency. It further appears that the minor fall of temperature in 1946—48 in the case of most species coincides with a decrease in numbers. These species finally show a frequency minimum during the period 1927—30 in spite of the fact that the minimum temperature for these 4 winters is comparatively high, but it must be admitted that one of these winters (1928/29) was a very severe ice-winter with a temperature of  $-0.8^{\circ}\text{C}$ . for January-March. The graphs of fig. 3 show that frequency minima of these species may also occur outside periods with severe ice-winters, but of course other factors than severe cold in winter will be able to reduce the frequency. The fact that the cold winters of 1940—42 were accompanied by frequency minima for all species clearly shows that these species cannot very well endure severe cold of winter.

Also the geographical distribution of the species goes to show that they cannot endure severe ice-winters; none of them live in arctic waters (at Greenland or the arctic shores of Europe).

Other species examined showed no frequency minimum during the severe ice-winters of 1940—42:

TABLE 2.  
Catch of species per 1/2 hour in eel-trawl in the various areas in year-periods between 1927 and 1950.  
M. = means for all years.

Area...	N	K	S	L	TV	H	Total	Area...	N	K	S	L	TV	H	Total
<i>Nassa reticulata</i>								<i>Portunus holsatus</i>							
1927-30	24	5.7	5.5	4.1	3.7	1.3	7.5	1927-30	3.5	0.6	0	..	..	..	1.4
1931-33	25	51	11	14	11	8.1	20	1931-33	8.0	0.7	0	..	..	..	3
1934-36	17	24	27	6.4	11	7.4	16	1934-36	2.0	0	0.1	..	..	..	0.7
1937-39	17	20	9	6.7	5.3	3.5	10	1937-39	10	0	0	..	..	..	3
1940-42	10	11	1.7	2.8	0.7	5.4	5.2	1940-42	0	0	0	..	..	..	0
1943-45	13	21	17	5.3	4.0	6.0	11	1943-45	3.3	0.1	0	..	..	..	3
1946-48	1	0.5	0.9	0.2	1.1	2.8	1.1	1946-48	0.2	0	0	..	..	..	0.1
1949-50	4.5	5.5	2.1	1.9	3.3	0.8	3.1	1949-50	12	1.3	0.5	..	..	..	4.6
M....	14	17	9	6	5	4	9	M....	5	0.3	0.1	0	0	0	0.9
<i>Buccinum undatum</i>								<i>Portunus depurator</i>							
1927-30	19	2.5	7.5	8	9	5.2	9	1927-30	2.8	0	0	..	..	..	0.9
1931-33	21	29	33	13	18	11	21	1931-33	0	0	0.1	..	..	..	0.03
1934-36	14	11	16	4.8	7.7	1.0	9	1934-36	2.4	0	0.1	..	..	..	0.8
1937-39	16	4.8	22	8.3	0.1	0	5	1937-39	0	0	0	..	..	..	0
1940-42	6	10	10	6.7	3	0	6	1940-42	0	0	0	..	..	..	0
1943-45	14	50	44	21	3.8	6.3	23	1943-45	0.3	0	0	..	..	..	0.1
1946-48	3	10	4.1	1.7	0.1	4.3	4	1946-48	0.8	0	0	..	..	..	0.3
1949-50	6.8	6.6	5.9	1.7	0.2	0	4	1949-50	13	0.5	0	..	..	..	4
M....	13	15	18	8	5	4	11	M....	2	0.06	0.03	0	0	0	0.7
<i>Philine aperta</i>								<i>Hyas araneus</i>							
1927-30	0	0.1	2.5	0	0	0.8	0.7	1927-30	0.5	0.01	..	..	..	..	0.3
1931-33	0	56	350	13	3.1	0.1	62	1931-33	2.7	0	..	..	..	..	1.4
1934-36	1.0	18	12	16	3.8	0	9	1934-36	0.3	0	..	..	..	..	0.2
1937-39	0	7.3	36	18	17	26	17	1937-39	0.1	0	..	..	..	..	0.05
1940-42	0	2.0	1.7	0.1	7	25	6	1940-42	0	0	..	..	..	..	0
1943-45	0	14	4.7	0.1	3.3	4.2	4	1943-45	0	0	..	..	..	..	0
1946-48	0	61	146	0.7	0.8	0.5	35	1946-48	0.1	0	..	..	..	..	0.05
1949-50	0.6	250	417	0.5	0	0	111	1949-50	0.1	0	..	0.03	..	..	0.05
M....	0.3	51	120	6	4	7	31	M....	0.5	0.01	0	0.01	0	0	0.25
<i>Mytilus edulis</i> (litres)								<i>Stenorhynchus rostratus</i>							
1927-30	1.2	17	11	35	12	69	24	1927-30	0.5	2.5	5.1	3.1	4.4	3.4	3
1931-33	1.9	13	8.4	70	62	52	35	1931-33	6.7	7.2	16	9	10	15	11
1934-36	0.2	57	35	8	49	13	29	1934-36	2.0	6.0	14	7	71	4.2	17
1937-39	0.1	8	43	8.7	9	3.4	12	1937-39	2.3	7.3	9	5	6	1.2	5
1940-42	0.1	62	15	17	84	53	39	1940-42	0.3	3.0	1	0.5	2.3	0.2	1.2
1943-45	15	69	68	49	257	124	97	1943-45	7.5	6.7	22	7.4	16	5.2	11
1946-48	0.1	37	33	12	28	65	28	1946-48	2.3	4.0	4	9	9	10	6
1949-50	0.3	39	18	5	27	9	16	1949-50	0.9	4.0	12	7.3	1.4	4.4	5
M....	2	38	29	26	66	47	35	M....	3	5	10	6	14	5	7
<i>Carcinus maenas</i>								<i>Eupagurus bernhardus</i>							
1927-30	4.3	24	4.8	4.8	6	1.4	8	1927-30	6	0.3	0.03	0.1	0.1	0	1.2
1931-33	8.9	10	16	7	3.5	19	11	1931-33	29	2.1	2.0	1.0	0.1	0	6
1934-36	11	40	21	8.3	17	10	18	1934-36	11	2.4	0.8	0.6	0.03	0	2.5
1937-39	9	20	21	8.3	6	18	14	1937-39	19	4.9	0.9	0	0	0	4
1940-42	7	18	16	8.4	15	45	18	1940-42	4	0.4	0.8	0.1	0	0	0.9
1943-45	13	17	17	9	11	57	21	1943-45	21	0.2	0.1	0	0.1	0	4
1946-48	13	20	30	8.7	9	14	16	1946-48	21	0.1	0.3	0.1	0.03	0	4
1949-50	33	69	66	15	39	12	39	1949-50	17	1.5	0	0.4	0.1	0	3
M....	11	27	22	9	13	22	17	M....	16	2	0.6	0.3	0.6	0	3

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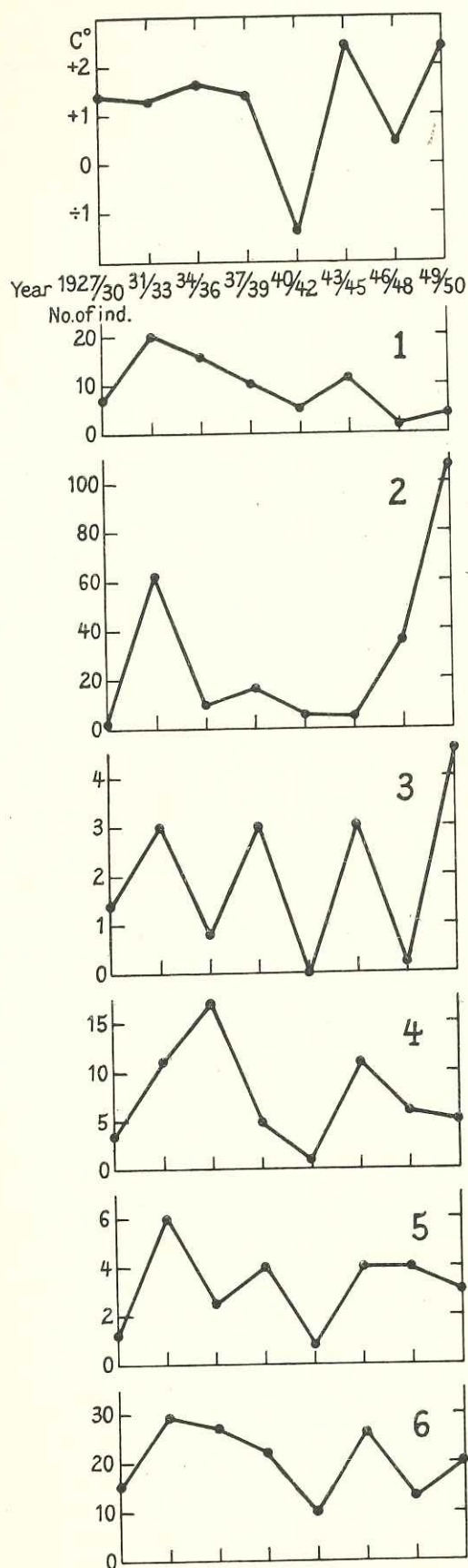
TABLE 2 (continued).

Area...	N	K	S	L	TV	H	Total	Area...	N	K	S	L	TV	H	Total
<i>Crangon vulgaris</i>								<i>Psammechinus miliaris</i> (continued).							
1927-30	15	16	43	21	16	31	24	1943-45	13	49	14	34	23	35	26
1931-33	33	64	102	32	166	103	83	1946-48	2	6	9	26	16	20	13
1934-36	14	63	72	31	106	19	51	1949-50	0.03	31	38	18	18	14	20
1937-39	31	35	55	66	60	30	46	M....	6	22	26	30	20	15	20
1940-42	26	43	76	23	29	53	42	<i>Metridium dianthus</i>							
1943-45	22	21	46	41	42	63	23	1927-30	4	9	15	24	12	7	12
1946-48	15	21	10	20	8	14	13	1931-33	7	14	11	16	64	14	19
1949-50	11	15	33	16	23	17	19	1934-36	8	9	19	8	44	10	16
M....	21	35	55	31	56	41	40	1937-39	6	13	13	10	7	8	10
<i>Asterias rubens</i>								1940-42	8	8	33	12	7	9	13
1927-30	140	68	81	13	12	7	69	1943-45	10	14	34	12	8	16	16
1931-33	134	99	115	18	40	15	71	1946-48	2	3	9	4	4	3	4
1934-36	74	112	63	19	48	8	54	1949-50	1.6	5	15	4	6	1.3	6
1937-39	43	145	62	19	4	31	51	M....	6	9	19	12	19	9	13
1940-42	70	60	79	18	23	13	44	<i>Ascidella aspersa</i> (litres)							
1943-45	34	59	54	26	42	22	40	1927-30	0.6	3	1.5	0.1	0	0	0.8
1946-48	19	17	37	23	13	20	23	1931-33	15	4	4	0.1	0	0	4
1949-50	76	69	34	18	45	8	42	1934-36	5	8	6	0.1	0	0.2	3
M....	74	79	66	19	28	16	47	1937-39	0.4	0.7	0.6	0	0	0.2	0.4
<i>Ophiura texturata</i>								1940-42	10	5	0.4	0.3	31	0	3
1927-30	89	68	61	35	31	94	63	1943-45	87	60	44	30	28	9	43
1931-33	116	491	224	113	123	65	189	1946-48	13	6	25	0.7	0.1	1.4	8
1934-36	13	218	273	77	461	159	200	1949-50	5	19	91	18	15	12	27
1937-39	43	84	343	175	55	102	134	M....	17	13	21	6	9	3	12
1940-42	205	91	345	63	231	42	163	<i>Cancer pagurus</i>							
1943-45	97	150	201	141	145	215	158	1927-30	0.1	0.2	..	..	..	..	0.2
1946-48	13	87	80	46	9	61	49	1931-33	0.2	0	..	..	..	..	0.1
1949-50	98	74	875	62	103	42	209	1934-36	0.1	0	..	..	..	..	0.05
M....	84	158	300	89	145	98	146	1937-39	0	0	..	..	..	..	0
<i>Psammechinus miliaris</i>								1940-42	0.2	0	..	..	..	..	0.1
1927-30	13	11	8	25	22	11	15	1943-45	0.1	0	..	..	..	..	0.05
1931-33	9	27	24	65	31	19	29	1946-48	0.2	0	..	..	..	..	0.1
1934-36	4	21	44	39	21	7	27	1949-50	0	0	..	..	..	..	0
1937-39	0.7	23	68	23	4	13	22	M....	0.1	0.03	..	..	..	..	0.07
1940-42	2.5	7	5	17	27	1	10								

*Buccinum undatum*, *Mytilus edulis*, *Carcinus mænas*, *Leander adpersus*, *Asterias rubens*, *Ophiura texturata*, *Metridium dianthus* and *Ascidella aspersa*. 4 of these 8 species (*Buccinum undatum*, *Mytilus edulis*, *Asterias rubens* and *Metridium dianthus*) are found as far northwards as Greenland, i. e. in arctic waters, and 2 others (*Carcinus mænas* and *Ophiura texturata*) advance as far as Iceland. In the case of these 6 species there is in other words an accordance between their impassivity to severe ice-winters and their geographical distribution. *Ascidella aspersa* and *Crangon vulgaris*, however, are found neither in arctic waters

nor at Iceland. Judging from their geographical distribution they should accordingly be as sensitive to cold as the species showing frequency minima in the Limfjord in ice-winters; in other words their fluctuations in the Limfjord and their geographical distribution are out of harmony.

The two economically most important crustacea of the Limfjord, lobster and prawn, are taken in so small numbers in the eel-seine, that their frequency cannot be estimated on this basis, but the variations in the yields of the fisheries speak of their changing frequency through the years. The following table



gives the annual mean catches in metric tons for the same periods as the other animals:

	Lobster	Prawn
1927—30 .....	15	19
1931—33 .....	15	21
1934—36 .....	9	19
1937—39 .....	10	6
1940—42 .....	3	2
1943—45 .....	4	1
1946—48 .....	6	6
1949/50 .....	12	5

In other words the yields of both of these fisheries are very small in the years with the severe ice-winters (1940—42), amounting to only  $\frac{1}{3}$  of the yield of the period immediately before. During the following period it is comparatively low, too, but in the case of the prawn it rises again in the years after 1946, while the increase of the lobster does not appear until 1949.

The Danish waters are near the northern limit of both of these species. None of them are found at the Faroes or Iceland; at Norway the lobster does not advance farther than off Lofoten while the prawn is not found north of Bergen. The shortness of the stocks in the years after the severe ice-winters is apparently a consequence of the fact that they had been reduced to such an extent that some years had to pass before they could be restored by the upgrowth of the youngs. This goes well with the fact that the prawn, which grows to full size and maturity in the course of 1 or 2 years, gave considerably increasing yields already in 1946, while the lobster, which takes 6 years to grow up, did not show an unmistakable increase of yields until 1949.

In other words the severe ice-winters of 1940—42 and to a less degree the cold winters of 1928/29 and 1946—48 caused a marked decrease of temporary duration among several species of bottom inverte-

Fig. 3. Numbers of individuals taken per 30 minutes with the eel-seine in 3 years' periods compared to the temperature of the surface water at Oddesund in January-March.

1. *Nassa reticulata*, 2. *Philine*, 3. *Portunus holsatus*, 4. *Stenorhynchus rostratus*, 5. *Eupagurus bernhardus*, 6. *Psammecinus miliaris*.

Antal individer taget pr.  $\frac{1}{2}$  time i åletog i 3-årsperioder 1927—1950, sammenlignet med overfladevandets temperatur ved Oddesund i januar—marts i samme perioder (øverste kurve). Tallene til venstre for kurverne 1—6 angiver antal individer.

1 = *Nassa reticulata*, dværgkonk. 2 = *Philine*. 3 = *Portunus holsatus*, svømmekrabbe. 4 = *Stenorhynchus rostratus*, stankelbenskrabbe. 5 = *Eupagurus bernhardus*, eremitkrebs. 6 = *Psammecinus miliaris*, søborre.

brates, primarily the species of a more southerly occurrence. A corresponding decrease was not observed among the species that also live in arctic waters.

**b. The influence of the eel-grass disease on the frequency.**

As already mentioned the eel-grass disappeared from the greater part of the Limfjord in 1933 and although there have been some indications of a reappearance, the eel-grass—apart from a few limited brackish areas—is still absent in most of the fjord or is found only in thin and sparse patches, which can by no means be compared to the large, vigorous vegetations from before the spring of 1933.

We shall now try to establish whether any changes in the occurrence and frequency of some of the larger bottom invertebrates have taken place in connexion with the disappearance of the eel-grass. The eel-seine is not used—and was not used before 1933—within the vegetations of eel-grass, but in somewhat deeper water outside, and so the material can hardly tell us anything about the changes in the animal populations of the eel-grass area itself, but only whether the disappearance of the eel-grass has affected the stock of animals outside this area, in other words the animal population of the fjord in a more general sense.

C. G. JOH. PETERSEN & P. BOYSEN JENSEN<sup>1)</sup> have stated that the main nourishment of the marine animals in Danish waters is comminuted organic matter, which is eaten by smaller animals constituting the food of larger animals and so on. In comparing the production of eel-grass, marine algae and plants these authors considered it legitimate to maintain that the eel-grass was by far the most important producer of organic matter, so that the animal life of Danish waters, in other words also the fishes ultimately depend on the eel-grass as a food matter.

This theory, however, is contested by A. KROGH (1935)<sup>2)</sup> and STEEMANN-NIELSEN (1944)<sup>3)</sup>, who state that the detritus is eaten but not digested by the animals. In support of this STEEMANN-NIELSEN further says (translated from Danish), "It was a severe blow

to Petersen's hypothesis when the nearly total disappearance of the eel-grass from the Danish waters on account of an epidemic disease in the early thirties proved to have no actual influence on the amounts of fishes or their food animals. It is true that large amounts presumable of eel-grass detritus is still preserved in the Danish waters, but there is hardly any reason to discuss that until it has been proved that this indigestible matter is assimilated by the animals". Though it is not quite obvious what the author means by 'actual' influence and 'presumably of' eel-grass detritus (if detritus is preserved, a considerable part of it must necessarily originate from the eel-grass), it is clear that the author is of opinion that the fact that the fish population has not decreased considerably after the disappearance of the eel-grass shows that the eel-grass is not so very important to the animal life as supposed by C. G. JOH. PETERSEN. But this reasoning is not necessarily correct. A possible alternative is that the importance of the eel-grass in the food of the marine animals has now shifted to other organisms, stationary algae and plankton, which can now be produced in larger quantities because inorganic nutrients (nitrates and phosphates), which were formerly used by the eel-grass, are now accessible to other productions of plants. It should be remembered here that these very nitrates and phosphates at most seasons and in most places of Danish waters are in deficit, which means that they are absorbed as rapidly as they appear. The organic matter, which these other plants now produce, can be used by the animals to the same extent as that produced by the eel-grass. So there is no reason to expect a decrease of the fish population after the disappearance of the eel-grass even if the latter, as maintained by C. G. JOH. PETERSEN, should be the main producer of the food of the animals. Thus the development in our waters since 1933 does not constitute a proof against the theory of PETERSEN.

The eel-grass disappeared from the Limfjord in 1933, and the question now is whether a change can be traced in the amount of bottom animals in 1934 and the following years. In order to find out I have, for each of the species that are taken in the eel-seine, calculated the mean frequencies for the years 1927—33 (before the disappearance of the eel-grass), for 1934—39 (the years immediately after) and for the years 1946—50; the years 1940—45, in which the severe ice-winters can have affected the figures, were

<sup>1)</sup> C. G. JOH. PETERSEN & P. BOYSEN JENSEN: Valuation of the Sea. I. Rep. Dan. Biol. Stat. 20, 1911.

<sup>2)</sup> A. KROGH: Den produktøkonomiske vevirkning mellem nogle plante- og dyresamfund. Naturens Verden 19, 1935.

<sup>3)</sup> E. STEEMANN-NIELSEN: Havets Planteverden. Skr. udg. af Komm. f. Danmarks Fiskeri- og Havunders. No. 13, 1944.

TABLE 3.

The frequency of the species in various periods before and after the disappearance of the eel-grass.

	No. caught pr. 1/2 h.			Difference from 1927/33 to			
	1927/33	1934/39	1946/50	1934/39		1946/50	
				no.	%	no.	%
<i>Metridium dianthus</i> .....	15	13	5	÷ 2	÷ 13	÷ 10	÷ 67
<i>Buccinum undatum</i> .....	14	7	4	÷ 7	÷ 50	÷ 10	÷ 71
<i>Nassa reticulata</i> .....	13	13	2	..	0	÷ 11	÷ 85
<i>Philine</i> sp. ....	29	13	66	÷ 16	÷ 55	+ 37	+ 141
<i>Mytilus edulis</i> .....	litres 29	21	23	÷ 8	÷ 28	÷ 6	÷ 21
<i>Carcinus mænas</i> .....	9	16	25	+ 7	+ 78	+ 16	+ 178
<i>Stenorhynchus rostratus</i> .....	6	11	6	+ 5	+ 83	..	0
<i>Eupagurus bernhardus</i> .....	3	4	4	+ 1	+ 33	+ 1	+ 33
<i>Crangon vulgaris</i> .....	52	49	15	÷ 3	÷ 6	÷ 37	÷ 72
<i>Asterias rubens</i> .....	70	33	31	÷ 37	÷ 53	÷ 39	÷ 56
<i>Ophiura texturata</i> .....	117	167	113	+ 50	+ 43	÷ 4	÷ 3
<i>Psammechinus miliaris</i> .....	21	25	16	+ 4	+ 19	÷ 5	÷ 24
<i>Asciidiella aspersa</i> .....	litres 2	2	16	..	0	+ 14	+ 700

not included. The figures of table 3 represent the numbers (or litres) per 30 minutes. The species that were taken nearly exclusively in Nissum Br., and the occurrence of which in the Limfjord is therefore highly dependent on an immigration through the Thyborøn Kanal, were not counted; they are rare crustacea like *Portunus holsatus*, *P. depurator*, *Cancer pagurus* and *Hyas araneus*.

If we begin with the difference between the periods 1927—33 and 1934—39, i. e. from the years before to the years immediately after disappearance of the eel-grass, we find that out of the 13 species mentioned 6 show a decrease in frequency: *Buccinum undatum*, *Philine*, *Mytilus edulis*, *Asterias rubens*, *Metridium dianthus* and *Crangon vulgaris*, the decrease of the two last-mentioned species, however, being so small that it may be considered unimportant. In other words only 4 of the 13 species show a distinct fall in numbers after the disappearance of the eel-grass. 10 years later, in the period 1946—50, 8 species show a fall in comparison to the time before the disappearance of the eel-grass, first and foremost all the species that showed a decrease in the 1934—39 period with the exception of *Philine*, which now shows a great + in frequency. The new species are *Ophiura texturata*, the decrease of which however, is insignificant, *Nassa reticulata* which showed no change in frequency in 1934—39 but a marked decrease in 1946—50, and finally *Psammechinus miliaris* with a decrease of only 24 %. For the mussel the decrease is comparatively small in both periods, only 28 and 21 %, respectively.

Of species showing an indisputable decrease of frequency after the disappearance of the eel-grass there remain the following 4 (the two figures represent the decrease in per cent. from 1927—33 to 1934—39 and to 1946—50):

<i>Buccinum undatum</i> .....	— 50	— 71
<i>Asterias rubens</i> .....	— 53	— 56
<i>Metridium dianthus</i> .....	— 13	— 67
<i>Crangon vulgaris</i> .....	— 6	— 72

Other species, however, show a distinct increase in number during the same periods:

<i>Carcinus mænas</i> .....	+ 78	+ 178
<i>Stenorhynchus rostratus</i> .....	+ 83	0
<i>Asciidiella aspersa</i> .....	+ 14	+ 1,700

In other words there are no indications of a general decrease in the production of the fjord as a whole after the disappearance of the eel-grass, or rather of the fjord outside the eel-grass area, neither do the yields of fishery show such a decrease. The following figures represent the annual mean yields in metric tons during periods before and after the disappearance of the eel-grass:

	Plaice	Cod	Eel in seine, on fork or hook	Fishes + crustaceans	Fishes minus herring and sprat, + crustaceans
1927—33	706	124	512	3,866	2,206
1934—39	404	91	496	3,012	1,698
1946—49	613	105	465	4,544	2,156

The decrease observed for plaice, cod and eel is small and not necessarily connected with the dis-

appearance of the eel-grass; it is more probable that it is due to the general and gradual overfishing in the fjord. The last column of the table, which includes all bottom fishes + crustaceans—i. e. the first animals to be supposed to suffer—show a decrease of quite negligible size-order. For fishes + crustaceans in general—in other words including the pelagic species herring and sprat—recent years even tell of an increasing yield as compared to the years before 1934.

Accordingly, neither the larger bottom invertebrates nor the fishes can be proved to show a general decrease of production during the years after the disappearance of the eel-grass. But 4 species of invertebrate bottom animals have decreased decidedly since the disappearance of the eel-grass: *Buccinum undatum*, *Metridium dianthus*, *Asterias rubens* and *Crangon vulgaris*. The problem is whether this decrease is casual or bears any causative relation to the disappearance of the eel-grass, i. e. whether any particular traits in the biology of these species make them dependent on the eel-grass. From the size of a few millimetres the youngs of *Buccinum undatum* and *Asterias rubens* lead a free life on the bottom, and it is very probable that this tiny fry in settling on the bottom require a somewhat harder support in order not to be overcome by the layer of soft ooze. Such harder places are found on the leaves of the eel-grass, and as a matter of fact the tiny star-fish are often found to sit in large quantities on the leaves of the eel-grass. In deeper water outside the eel-grass zone the valuations with the Petersen bottom sampler produce surprisingly few quite young individuals of whelk and star-fish, much fewer than would be expected from the numbers of bigger individuals. So there is any reason to suppose that the very young individuals preferentially live in the zone and on the leaves of the eel-grass and gradually emigrate towards deeper water. The decrease in the numbers of these two animals after the disappearance of the eel-grass may accordingly be due to a serious deterioration in the living conditions of their youngs.

This explanation, however, does not apply to the shrimp, which is a swimming animal throughout its life and not particularly identified with the eel-grass, or to the sea-anemone, which is sedentary or at any rate creeping so slowly that even shorter migrations are out of the question.

After all, then, we have little support for the belief that the decrease in frequency of these 4 species is

connected with the disappearance of the eel-grass. As often during biological investigations in nature we must confine ourselves to the statement that there is a coincidence in time of fluctuations.

As mentioned above the present material from the eel-seine fishings does not tell us how the animals living within the eel-grass area have reacted on the disappearance of the eel-grass. But the statistics of "Fiskeriberetningen"<sup>1)</sup> on the yields of the prawn convey an idea of the fluctuations in frequency of the prawn (*Leander adspersus*), an animal that is so closely connected with the eel-grass.

In periods before and after the disappearance of the eel-grass the annual mean-catches of prawn in the Limfjord were:

1927—33 .....	20 tons
1934—39 .....	13 -
1946—49 .....	6 -

A considerable part of the prawns that are caught in one year were hatched the year before, and so it is considered legitimate to include the catching year 1934 in the period before the disappearance of the eel-grass:

1927—34 .....	21 tons
1935—39 .....	10 -
1946—49 .....	6 -

In a different wording there is a very marked decline of the yields after the disappearance of the eel-grass. It remains to decide whether this means a decrease in the quantity of prawns or only a spreading of the prawns over the fjord—because their proper habitat, the eel-grass, disappeared—so that it became more difficult to fish them. One would expect such a spreading to be mirrored in an increasing number of prawns taken in the eel-seine, which is used scatteredly all over the fjord, although this increase must be a limited one because the prawns from the comparatively narrow eel-grass zone must have spread over the many times larger areas without. During periods before and after the disappearance of the eel-grass the following mean numbers were taken per 30 minutes in the eel-seine:

1927—33 .....	0.06
1934—39 .....	0.60
1946—50 .....	0.03

In the very years 1934—39 the numbers of prawns taken in the eel-seine rose considerably, a fact that

<sup>1)</sup> Published yearly by the Danish Ministry of Fisheries.

speaks in favour of such a spreading over the fjord. The eel-grass disappeared from the Limfjord in the spring and early summer of 1933; in accord with this fact no prawns were taken in deeper water in the spring while no less than 0.7 were captured per 30 minutes in the autumn of 1933.

In the individual years of the 1933—39 period the following numbers of prawns were taken in the eel-seine per 30 minutes:

1933 .....	0.4
1934 .....	2.9
1935 .....	0.4
1936 .....	0.1
1937—39 .....	0

This means that the great majority were taken in the year after the disappearance of the eel-grass while the years 1935 and 36 yielded much fewer and 1937—39 none whatever. This seems to indicate that the prawns with the disappearance of the eel-grass spread over vaster areas, but did not find conditions sufficiently good in the new surroundings, which led to a decrease in number.

Accordingly, a very great reduction of the prawn population of the fjord took place in the years after the disappearance of the eel-grass, and the fact that the prawns are so closely connected with the eel-grass gives reason for the belief that the decrease is a consequence of the disappearance of the eel-grass.

At the coasts of the Kattegat and the more open coasts of the northern and central part of the Belt Sea the eel-grass also disappeared in 1933. The sub-joined table gives the annual mean catches of prawns in tons from the waters inside the Skaw before and after the disappearance of the eel-grass:

	1927/33	1934/39	1946/49
Kattegat.....	21	20	30
Belt Sea.....	82	217	251
Sound.....	3.4	10	12
Western Baltic.....	6	21	35
Proper Baltic.....	1.6	5	6

In the Kattegat there is a slight fall during the first years, but a rapid rise later on. In the other waters we find a marked increase in both periods after the disappearance of the eel-grass: in these figures there is nothing to indicate a decrease of the prawn population since 1933. On the other hand the figures of the catches cannot give a clear idea of the fluctuations of the stock because the prawn fishery

was intensified very much in these waters in the beginning of the thirties when seine fishing for prawn in deeper water and also during most of the winter half-year became common. Finally it should be remembered that only the Kattegat in its full extent with the exception of the inner parts of the Isefjord and the Roskildefjord was attacked by the disease while large areas of the Belt Sea, especially fjords and creeks, the preferred habitat of the prawn, were spared together with the southernmost part of the Belt Sea and the western and proper Baltic. Therefore the catch figures from these waters do not clearly describe the reaction of the prawn population on the disappearance of the eel-grass. The fact, however, that the yield in the Kattegat rose by only 50 %, while in other waters that were less exposed to or not affected at all by the eel-grass disease it rose to quadruple the amount, may be considered a proof that the disappearance of the eel-grass has damaged the prawn population also outside the Limfjord.

#### 4. The larger bottom invertebrates in the fishery.

Among the larger bottom invertebrates lobster, prawn, mussel and star-fish are objects of commercial fishing. Lobster and prawn have been fished from old times; the mussel fishery is somewhat newer, about 30 years old, and the star-fish fishery is only about 2 years old. The following figures represent the yields of these fisheries in annual means for 1948 and 49 (for star-fish only 1949 because this fishery was only begun in the course of 1948):

Lobster.....	10 tons	90,000 kr.
Prawn.....	7 —	36,000 —
Mussel.....	8,200 —	288,000 —
Star-fish.....	2,100 —	147,000 —
Total...	10,317 tons	561,000 kr.

The total annual yield of the Limfjord fisheries in the same years was 13,590 tons and 5,754,000 Dan. kroner. In other words lobster, prawn, mussel and star-fish constitute  $\frac{3}{4}$  of the weight yield and  $\frac{1}{10}$  of the value. In value they nearly equal the plaice fishery, and in weight the amount of invertebrates taken in the fisheries totals three times the fishes. In the household of the fjord (the consumption of nutrients) the fishing of bottom invertebrates thus plays a far more prominent part than the catches of fish.

The two old fisheries, the lobster and prawn fisheries, have decreased very much in the course of time; it has already been mentioned that the prawn population was seriously damaged both by the disappearance of the eel-grass and by the severe ice-winters in 1940—42 and that the lobster population suffered very much during these ice-winters. It will of course be interesting to examine whether the fishery in itself has also damaged the stocks of these valuable crustacea, i. e. whether these stocks are being overfished. The following figures give the annual mean catches in tons from 5 years' periods after 1891:

	Lobster (hummer)	Prawn (reje)
1891—95 .....	?	25
1896—1900 .....	23	31
1901—05 .....	15	35
1906—10 .....	14	25
1911—15 .....	19	23
1916—20 .....	10	26
1921—25 .....	10	5
1926—30 .....	16	15
1931—35 .....	12	21
1936—40 .....	10	6
1941—45 .....	5	2
1946—49 .....	7	6

Thus both fisheries have decreased very much since the end of the last century, the lobster fishery from 23 to 7, the prawn fishery from 31 to 6 tons. The lobster fishery began to decline already about 1901—05, the prawn fishery as late as 1919—20; both fisheries rose somewhat in 1926—35, but in 1936—40 there was a slight fall in the lobster fishery and a very rapid one in the prawn fishery (the latter due to the disappearance of the eel-grass). The years 1941—45 brought another enormous deterioration of both fisheries (the severe ice-winters). In 1946—49 there was another rise of the yields which, however, did not by far reach the figures from before 1935.

It is particularly worth noting the very low yield of the prawn fishery in the 5 years' period 1921—25, only 5 tons. The statistics for the individual years show that this period of low yields goes from 1919 to 1927, i. e. 9 years with a yield per annum of only 5 tons against 27 tons annually in the previous and 21 tons in the following 9 years. The very low yield of this period can hardly—at least not in any considerable degree—be due to a too intense fishing because the fall at the beginning and the rise at the end of the period are very steep. The cause is more

likely to be unfavourable changes in the conditions of living, more particularly (because the prawn in Danish waters lives near the northern limit of its habitation) in the conditions of temperature either in winter or during the time at which the fry is developed (May-June).

In the following table the yields of the prawn fishery for the 3 periods is compared to the temperature of the surface water at Oddesund in January-February and in May-June:

	Tons	°C. Jan.-Feb.	°C. May-June
1910—18 .....	27	0.9	13.4
1919—27 .....	5	1.1	12.3
1928—36 .....	21	1.1	13.1

The winter temperature is nearly the same for the three periods, but the temperature in early summer was 1° lower in the poor catching period than in the two good periods. So there is no doubt some justification for connecting the low temperature in early summer with the low catch yields.

Consequently, the decrease in the yield of the prawn fishery during these 30 years to a considerable extent must be put down to unfavourable conditions: 1) the disappearance of the eel-grass, 2) severe ice-winters, and 3) comparatively low summer temperatures.

A look at figure 4, which illustrates the yield of the prawn fishery through the whole period 1890—1950, will show that the decrease appeared also before 1918, and it is further seen that the summits of the graph illustrating the catches, the years with the highest yields, are growing constantly lower throughout the period. This decrease during the whole long period is possibly due to a too intense fishing; but the very abrupt and catastrophic falls of the yield in the beginning of the twenties, the end of the thirties and throughout the forties must be set down to unfavourable natural conditions.

Earlier authors<sup>1)</sup> have been maintained that a too intense fishing has caused the periodically failing yield of the prawn fishery; but this is not the main cause, which also appears from the fluctuations in the yield of the prawn fishery in the Belt Sea + the

<sup>1)</sup> TH. MORTENSEN: *Undersøgelser over vor alm. Rejes Biologi og Udviklingshistorie etc.* Udg. af Dansk Fiskeriforening 1897.

C. G. JOH. PETERSEN: *The Yield of the Prawn Fishery from 1885—1907 and its Improvement by Means of Protection.* Rep. Dan. Biol. Stat. 18, 1909.

western Baltic (see fig. 4). In spite of a long period of intense prawn fishing we now find the yields in these waters to be as high as ever. It is further seen that down to the beginning of the thirties the two

It is seen that in both areas severe winters are followed by light yields of the prawn fishery.

Accordingly, the shorter periods showing very light catches of prawn are hardly caused by too intense

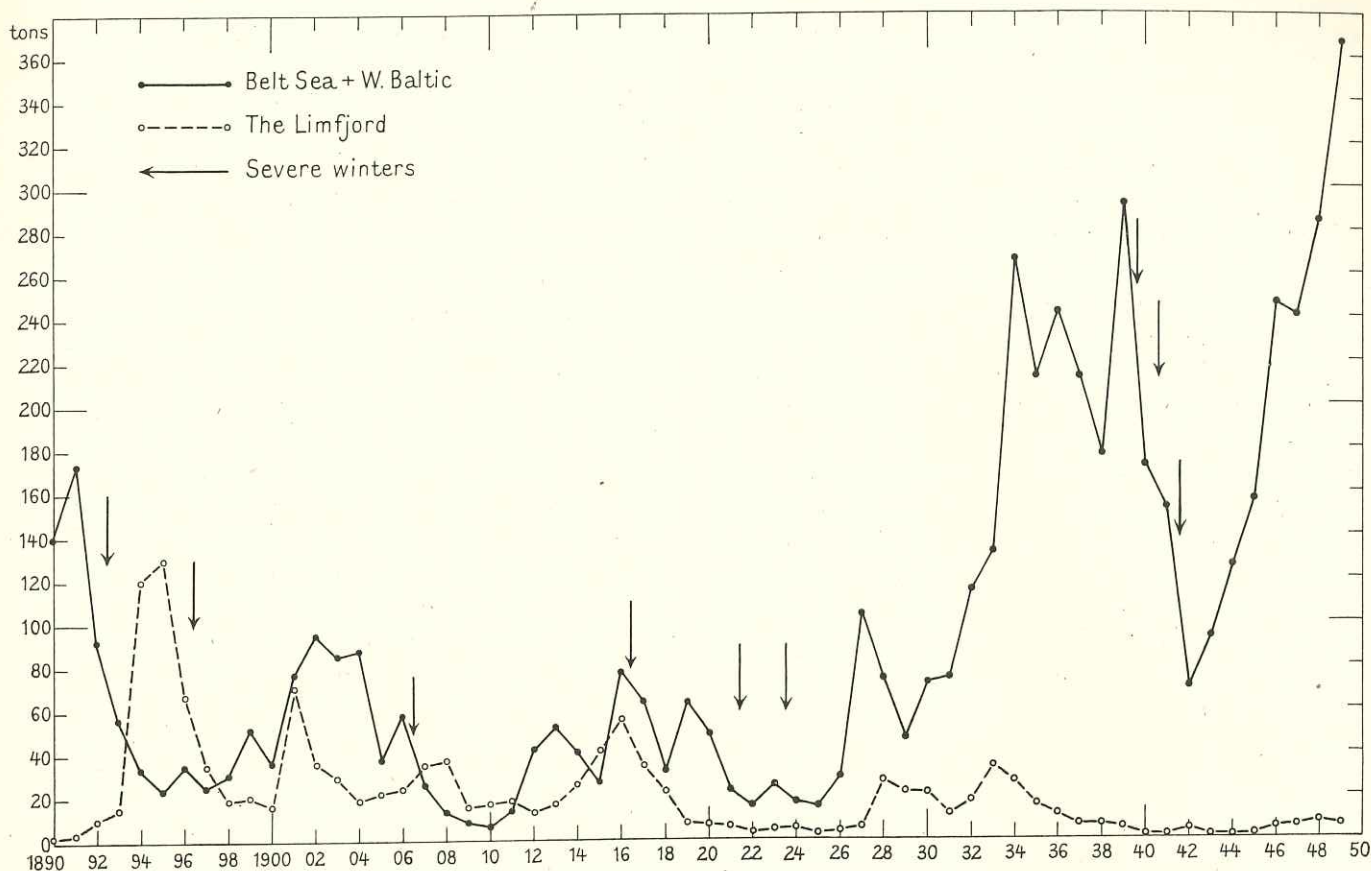


Fig. 4. The yield of the fishery of the common prawn (*Leander adspersus*) in the Belt Sea + the western Baltic and in the Limfjord 1890—1950.

Udbyttet af fiskeriet 1890—1950 efter almindelig reje (*Leander adspersus*) i Bælthavet + Vestlige Østersø (fuldt optrukket kurve) og i Limfjorden (brudte kurve). De lodrette pile angiver år med strenge vintre.

graphs are collateral and that all three waters yielded small catches during the severe ice-winters 1940—42. The difference between the waters is that whereas the yield in the Limfjord decreased heavily during the years after the disappearance of the eel-grass the Belt Sea and the western Baltic showed no decrease (on the contrary!), and as already mentioned this is explained by the fact that the prawn areas of these waters have been attacked by the eel-grass disease to a smaller extent only.

In the figure severe winters are marked by means of arrows (the arrows are found 6 months previous to the calendar year in question, the arrow for the severe ice-winter 1893 was put between 92 and 93).

fishing, but rather by unfavourable natural conditions. As to the Limfjord, however, the uniform fall of the graph illustrating the yield goes to show that at any rate in this water there has been some overfishing.

The decrease in the lobster fishery of the Limfjord has not been so great as that of the prawn fishery but more uniform and without the great fluctuations of the latter. Since 1920 the lobster-pot has been nearly the only gear in use and has not been altered from then till now, and so the quantity of lobster caught per 1 lobster-pot can be considered representative of the fluctuations of the stock. In 4



years' periods the annual mean catches per 1 lobster-pot were as follows:

1920—23	4.1 kg	1936—39	2.5 kg
1924—27	3.6 -	1940—43	1.6 -
1928—31	3.2 -	1944—47	2.4 -
1932—35	2.7 -	1948/49	4.2 -

It is seen that the catch per 1 lobster-pot has decreased from 1920—23 to 1936—39. This smooth fall can hardly be explained in any other way than by the fact that the fishery was too intense for the stock. During and after the severe ice-winters of 1940—42 there was a much more rapid decrease, as mentioned apparently in consequence of the lobster not being able to endure the severe winter cold. During recent years the stock has revived to some extent.

The decrease in the yield of the prawn fishery is primarily due to unfavourable changes in the natural conditions and not so much to overfishing, but as far as the lobster fishery is concerned the decrease is caused first and foremost by overfishing. The stock cannot endure the intense fishing to which it has been and is exposed, and more effective measures of protecting this valuable crustacean are therefore necessary.

About the mussel it was said (p. 27) that it decreased little in quantity during the years immediately after the disappearance of the eel-grass and that no decrease at all took place during the severe ice-winters. The mussel fishery began to gain importance during the first world-war. In 1918 the yield is given for the first time in Fiskeriberetningen (the Fisheries Report); it was then 1,640 metric tons. During the years after that war the yield fell rapidly, and it was not until 1925 and 26 that it exceeded 1,000 tons. From 1927 to 1939 the yield ranged between 1,500 and 2,500 tons, but afterwards it rose rapidly:

1940	6,849 tons	1946	1,637 tons
1941	7,365 —	1947	955 —
1942	22,916 —	1948	3,681 —
1943	85,250 —	1949	12,725 —
1944	53,306 —	1950	17,666 —

During the second world-war, when the demand was very great, the yield rose enormously; after this

war it fell once more, but has begun to rise again during these late years.

The fluctuations of the yield are so abrupt and great, that they cannot be due to changes in the size of the stock, but must be put down to rises and falls in the demand. Nevertheless the question arises whether the mussel population of the fjord for a lengthened period will be able to endure the intense fishing. During the fishing experiments with the eel-seine the following quantities in litres per 30 minutes were taken in 3 years' periods since 1927:

1927—29	9 l	1939—41	26 l
1930—32	53 -	1942—44	85 -
1933—35	18 -	1945—47	53 -
1936—38	21 -	1948—50	15 -

In 1927—38 when the mussel fishery was small, ranging between 1,500 and 2,500 tons, the catches per 30 minutes in the eel-seine, which must be considered representative of the density and size of the stock, ranged between 9 and 53 l. In spite of the heavy commercial catches after 1939 the fluctuations in 30 minutes' hauls with the eel-seine were very much the same, 15—85 l, as in the years before 1939. Apparently the intense fishing has caused no damage to the stock. In 1945—48 the commercial fishing of mussel was inconsiderable (900—3,600 tons annually); nevertheless the eel-seine fishery of 1948—50 yielded only 15 l per 30 minutes, and so the nearly total protection of 1945—48 has caused no rise of the stock. In 1939—41, before the beginning of the intense fishing, the eel-seine brought out 26 l per 30 minutes, in 1945—47, at the end of it, 53 l per 30 minutes or much more than at the beginning of the fishery. This means that the extensive fishing has in no way diminished the stock; if anything, it seems to have created better conditions for the thriving of the mussels, and many things speak in favour of this possibility. Where they occur in so large quantities, that a fishing will pay, the mussels live on "beds", sitting close to each other or even in several layers. They are so densely crowded, that it must be difficult for the individual specimen to find its food, and what is more serious: to get the necessary oxygen for its respiration. In fact it is well-known that during the warm summer season when the water contains the smallest quantities of oxygen large amounts of mussels will die on the beds. In Thisted Br., for instance, the fishermen have observed that the mussels in summer sometimes die out over vast areas in

the course of very short time. These observations are confirmed by the investigations of the Biological Station: in places where a dense stock was living in June only dead or rotting mussels, were found in September. These mussels had not been attacked by a disease, which appears from the fact that the other bottom animals of the bed were killed during the same period. It is apparently a question of death of asphyxia; the mussels of the large beds have simply suffocated each other.

Though an intense fishing on limited mussel beds for a long period will of course bring about an essential reduction of quantity on the very bed, it does not seem likely that it will damage the stock as a whole; on the contrary it may even be of advantage to it. The thinning will bring the mussels better conditions of living—more oxygen, more food. More food means a more rapid growth of the mussel, i. e. a better article of trade, partly because there will be more flesh as compared to the shells, partly because the young mussels will not be so overgrown with other animals as the older mussels, thus getting a finer shell.

It is too early to say whether an extensive mussel fishery for a long period of years will imperil the stock, but so far at any rate there is no hesitation to pursue such a fishery in the fjord.

The fishing of star-fish (*Asterias rubens*) is of new date; it began in 1948. The gear used is a small but heavy trawl, which is spread by means of a pole of up to 4 m length. The fishery started in Løgstør Br. but is now pursued locally over large areas of the fjord. In 1949 the yield was 2,100 tons — 147,000 kr. The yield in 1950 was only 360 tons — 27,000 kr. The fishery is too young for us to say how it will affect the stock of star-fish. The fishing experiments of the Biological Station during recent years have given the following numbers of star-fish per 30 minutes:

	The whole fjord	Livø Br.
1943 .....	60	38
1944 .....	39	21
1945 .....	60	20
1946 .....	21	27
1947 .....	21	23
1948 .....	23	18
1949 .....	49	17
1950 .....	34	19

In the fjord as a whole there is no decrease in 1949 and 50. In Livø Br. there is a slight decrease,

but equally few individuals were taken in earlier years, and so the decrease is not necessarily caused by the fishery. The fishery may of course cause a local reduction: the fishermen of Løgstør have experienced that at the same places they could not by far take so many star-fish in 1950 as in 1948 and 49. But even then there is no ground for concern. The star-fish is one of the most noxious animals of the fjord, partly because it eats away the food of the bottom fishes, partly because it spoils the flat-fishes that are taken in the nets. The damage done in this way is decidedly of far greater extent than the yield of the star-fish fishery. The fisheries of the fjord as a whole will no doubt be interested in having as small a star-fish population as possible.

### 5. Concluding remarks.

The annual fluctuations in the amounts of larger bottom invertebrates in the Limfjord were estimated from the numbers of individuals taken in a fine-meshed trawl (eel-seine) in the years 1927—50. For the marketable ones also the figures of the catch yield from the Fisheries Statistics were considered.

Most of the species showed very great fluctuations from year to year in the catch figures. Some of these fluctuations may be due to insufficiency of the material, especially in the case of species occurring in small numbers; others are consequences of causes, changes in condition, that cannot be investigated; others again can be put down to demonstrable changes in the natural conditions or to the influence of the fisheries. Severe cold and ice-cover in winter have caused a decrease in the amount of a number of species: *Nassa reticulata*, *Philine* sp., *Psammochinus miliaris*, *Eupagurus bernhardus*, *Stenorhynchus rostratus*, *Portunus holsatus*, *P. depurator*, *Homarus vulgaris* and *Leander adspersus*.

The nearly total disappearance of the eel-grass from the Limfjord in 1933/34 caused no general reduction in the amount of bottom animals but the quantities of the following species, *Leander adspersus*, *Buccinum undatum*, *Asterias rubens*, *Metridium dianthus* and *Crangon vulgaris*, decreased perceptibly during the years after 1933/34. As regards the first three of these species it is an obvious conclusion that the decrease was caused by the disappearance of the eel-grass.

Several of the larger bottom invertebrates are the

objects of fishery. As far as the lobster is concerned the gradual decline of the yields tells us that this species has been and is exposed to a considerable overfishing, much to the damage of the stock and hence of the fishery. Also the prawn seems to suffer from some overfishing, but the extremely great fall of the yields during these 10—20 years to all essentials seems to be caused by unfavourable changes of condition (the disappearance of the eel-grass and, for a shorter period, the severe ice-winters or low temperatures during the spawning season).

Periodically, the mussel has been fished very extensively during the last 30 years, but in quantity it does not seem to have been affected by the fishery. The star-fish has been fished for only since 1948, and it is still too early to say anything about the influence of the fishery on the size of the stock.

During the past 25 years the weight yields of the fisheries (fishes + crustacea) in the rest of our waters have more than doubled, but in the Limfjord there has been a standstill: in 1925—29 4,400 tons, in 1945—49 4,450 tons annually. In other words the development of boats and gears that has taken place

in the Limfjord during the same period in contrast to other Danish waters has led to no increase at all of the catch yields. This is apparently due to the fact that the Limfjord with its limited extent and easy access to harbours and fishing areas was exposed to overfishing long before the rest of our waters.

The fish population of the Limfjord cannot endure a further development of the fishery and hardly even the present fishery. Therefore it is a step in the right direction that a fishing of different species of invertebrate bottom animals (mussel, star-fish) has started in the Limfjord during recent years, for here further development is possible. This is undoubtedly true of the mussel and star-fish fisheries, and other invertebrates like the whelk<sup>1)</sup> can possibly be included, too. If boats and material are used for these purposes, it will not only increase the yields together with the quantities landed, but it will also give some protection to the hard pressed fish population.

<sup>1)</sup> C. G. JOH. PETERSEN: Some Experiments on the Possibility of Combating the Harmful Animals of the Fisheries, especially the Whelks in the Limfjord. Rep. Dan. Biol. Stat. 19, 1911.

## Dansk oversigt.

### Vekslinger i hyppighed af større, hvirvelløse bunddyr i Limfjorden 1927—50.

De årlige svingninger i mængden af større hvirvelløse bunddyr i Limfjorden (se kortet fig. 1) er bedømt ud fra antallet af individer fisket med en finmasket trawl (åletog) under Biologisk Stations forsøgsfiskeri i årene 1927—50. For de arter, der er genstand for fiskeri: hummer, rejer, muslinger og korsfisk, er tillige fangsttallene i den af fiskeriministeriet offentliggjorte "Fiskeri-Beretning" benyttet.

Med hensyn til udbredelsen i fjorden kan de undersøgte arter stort set deles i 2 grupper (tab. 1 og fig. 2 a og b): en, hvis arter aftager i hyppighed fra vest mod øst, altså med aftagende saltholdighed, og en anden hvis arter forekommer nogenlunde lige talrigt gennem det undersøgte fjordområde, og som således er ret uafhængige af saltholdigheden. Arterne af denne anden gruppe lever da også langt ind i vore farvande, flere af dem endda ind i Østersøens brakke vand, hvorimod den første gruppes arter har deres indergrænser i vore farvande allerede i Kattegat eller Bælthavet.

For de fleste arters vedkommende er der fundet

meget store svingninger i fangsttallene fra år til år. Nogle af disse svingninger kan måske skyldes materialets utilstrækkelighed, dette må især gælde for de arter, der kun forekommer i ringe mængde, andre skyldes årsager, kårændringer, som ikke har kunnet efterforskes, medens endelig andre kan henføres til bestemte ændringer i de naturlige kår eller til fiskeriets indflydelse. Hård kulde og isdække om vinteren har bevirket en nedgang i mængden af en række arter (se tab. 2 og fig. 3), nemlig: Dvergkonk (*Nassa reticulata*), "finker" (*Philine*), søborre (*Psammechinus miliaris*), eremitkrebs (*Eupagurus bernhardus*), stankelbenskrabbe (*Stenorhynchus rostratus*), svømmekrabbe (*Portunus holsatus* og *P. depurator*) samt hummer (*Homarus vulgaris*) og reje (*Leander adspersus*). Disse arter har da også en mere sydlig udbredelse, idet ingen af dem lever i arktiske farvande, ved Europas ishavskyst eller ved Grønland.

Ålegræssets næsten fuldstændige forsvinden fra Limfjorden i 1933/34 medførte ikke nogen almindelig tilbagegang i mængden af bunddyr. Enkelte arters

individmængde formindskedes dog føleligt i årene efter (se tab. 3), nemlig rejen (*Leander adspersus*), konksnegl (*Buccinum undatum*), korsfisk (*Asterias rubens*), søanemone (*Metridium dianthus*) og hestereje (*Crangon vulgaris*). For de 3 førstnævnte arter, der enten som rejen så at sige hører hjemme i ålegræsset, eller som konksneglen og korsfisken som yngel sidder i stor mængde på ålegræssets blade, er der god grund til at antage, at tilbagegangen er forårsaget af ålegræssets forsvinden.

Flere af de større hvirvelløse bunddyr er genstand for fiskeri. For hummeren viser fiskeriudbyttets gradvise nedgang såvel som nedgangen i udbyttet pr. tejn (se teksttabellerne s. 30 og s. 32), at denne art har været og er genstand for en betydelig overfiskning til skade for bestanden og dermed for fiskeriet. For rejens vedkommende (se tabellen s. 30) synes der også at have været nogen overfiskning, men den overordentlig store nedgang i udbyttet gennem de sidste 10—20 år skyldes dog i alt væsentligt ugunstige ændringer i kårene (ålegræssets forsvinden og, for en kortere periode, de strenge isvintre eller lave temperaturer i yngletiden (se fig. 4 og tekstabel s. 30).

Blåmuslingen, der gennem de sidste 30 år periodevis har været genstand for et særdeles stærkt fiskeri (se teksttab. s. 32, der angiver fangsten i tons i årene 1940—50), synes ikke med hensyn til sin mængde at være påvirket af fiskeriet.

Korsfisken er kun blevet fisket siden 1948; der blev i 1949 fisket 2 100 tons = 147 000 kr., og endnu kan der ikke siges noget om fiskeriets indflydelse på bestanden i dens helhed; kun på de stærkest befiskede pladser synes der at være sket en tilbagegang i mængden.

Medens fiskeriudbyttet i vægt (fisk + krebsdyr) i vore øvrige farvande er mere end fordoblet i løbet

af de sidste 25 år, er udbyttet i Limfjorden uforandret i denne periode, i 1925—29 4 400 tons årligt, i 1945—49 4 450 tons. Den udvikling af fartøjer og redskaber, der er foregået på Limfjorden i de sidste 25 år, har altså ikke givet nogen som helst forøgelse af fangstmængden, således som det har været tilfældet i vore øvrige farvande. Dette skyldes åbenbart, at Limfjorden med sin ringe udstrækning og lette adgang til havne og fiskepladser langt tidligere er blevet genstand for overfiskning end vore øvrige farvande.

Naturligvis vil en udvikling af fiskeriet, d. v. s. en øgning af dettes udbytte kunne bæres af bestanden, såfremt denne forøges gennem omplantning og yngeludsætning. Med vor nuværende biologiske viden er det teknisk muligt at udklække, opdrætte og udsætte yngel af hummer (og rejer), og f. eks. af torsk og rødspætte i en sådan mængde, at et øget fiskeri vil blive resultatet; spørgsmålet er "bare", om det kan betale sig. Men uden en sådan særlig pleje i forbindelse med kraftige fredningsforanstaltninger tåler Fiskebestanden i Limfjorden ikke en yderligere udvikling af fiskeriet og vel næppe heller det fiskeri, den er genstand for nu. En vis fredning af de stærkt befiskede bestande og dermed et skridt i den rigtige retning er imidlertid allerede foretaget derved, at man i de senere år på Limfjorden har påbegyndt fiskeri efter forskellige arter af hvirvelløse bunddyr (muslinger, korsfisk); thi der er der visse muligheder for udvikling tilbage. Muslingefiskeriet og korsfiskeriet kan utvivlsomt udvikles yderligere, og måske kan også andre hvirvelløse dyr, f. eks. konksnegl, inddrages i fiskeriet. Ved at fartøjer og materiel sættes ind på dette fiskeri efter hvirvelløse bunddyr øges ikke blot udbyttet med de opfiskede mængder, men den hårdt trængte fiskebestand får derved en vis fredning.

## Two Danish Finds of Female Eel (*Anguilla anguilla*) in Spawning or Partial Spawning Dress.

By C. J. RASMUSSEN

WITH the termination in 1922 of JOHS. SCHMIDT's encircling of the spawning area of the European eel (*Anguilla anguilla*) in the western Atlantic a very important contribution had been added to our knowledge of the final phase of the life cycle of the eel, but at the same time JOHS. SCHMIDT's results gave rise to a number of questions which largely speaking are still unanswered. There is for instance still a large lacuna in our concrete knowledge of the migrations of the silver eel, its advancing sexual development and the factors stimulating the latter, its spawning and later fate after it has left the coasts of western Europe. In spite of the conspicuous morphological changes attending the process of sexual maturation observations of silver eel at a much more than normally advanced stage of maturation are very rare. JOHS. SCHMIDT (1906) described such a fully mature male eel caught in the Præstø Fjord in September 1903, the exterior deviations of which from the normal appearance of the silver eel had arrested attention. Besides by its highly developed sexual organs containing mature spermatozoa this fish was

especially conspicuous by its very large eyes and long, nearly black, pointed pectoral fins.

It is not until these late years that new Scandinavian finds of eel of a conspicuous phenotype have increased our knowledge of the metamorphosis distinguishing the silver eel stage from the spawning stage. These finds (SVÄRDSON, 1949) partly include two male eels showing the same exterior morphological changes as the Præstø Fjord eel though not being sexually mature like the latter, partly two female eels caught within the same period and also showing pronounced phenotypical deviations from normal silver eels. Besides the large eyes and long, pointed, dark-coloured pectoral fins all these eels showed a marked bronze coloration of venter and sides, and moreover one of the female eels was conspicuous by a total absence of fat. Like the male eels none of the females were mature though one of them contained somewhat larger eggs (0.3 mm in diameter) than are normally found in silver eels (0.1—0.2 mm). In eels treated with hormones (BRUUN, HEMMINGSEN & MØLLER-CHRISTENSEN, 1949) the

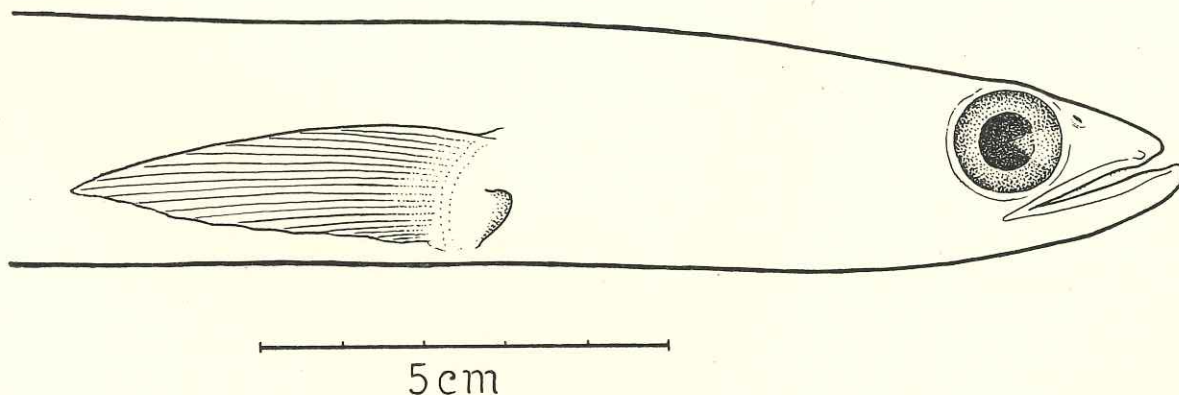


Fig. 1. Large-eyed female eel caught at the east coast of Samsø on September 29th, 1946 (P. H. WINTHER del.).

Storejet hunål fanget ved Samsøs østkyst den 29. september 1946.

average sizes of eggs hitherto reached are as much as 0.46 mm, and most probably the size order of mature eel eggs will prove to be about 1.0 mm in diameter.

In other words these eels are interesting not on account of their primary sexual development, but exclusively because they are the only female eels as far described in Scandinavia which in their exterior

pigment—also on the venter—but according to the information supplied the fish was originally stony-grey with a light venter as “commonly in silver eels”.

The width of the ovaries was 14 mm, the diameter of the eggs (after fixation) 0.25 mm.

2. Length 80 cm, weight 388 g. Caught (on hook) in the lake Furesø on August 19th, 1950 (fig. 2).

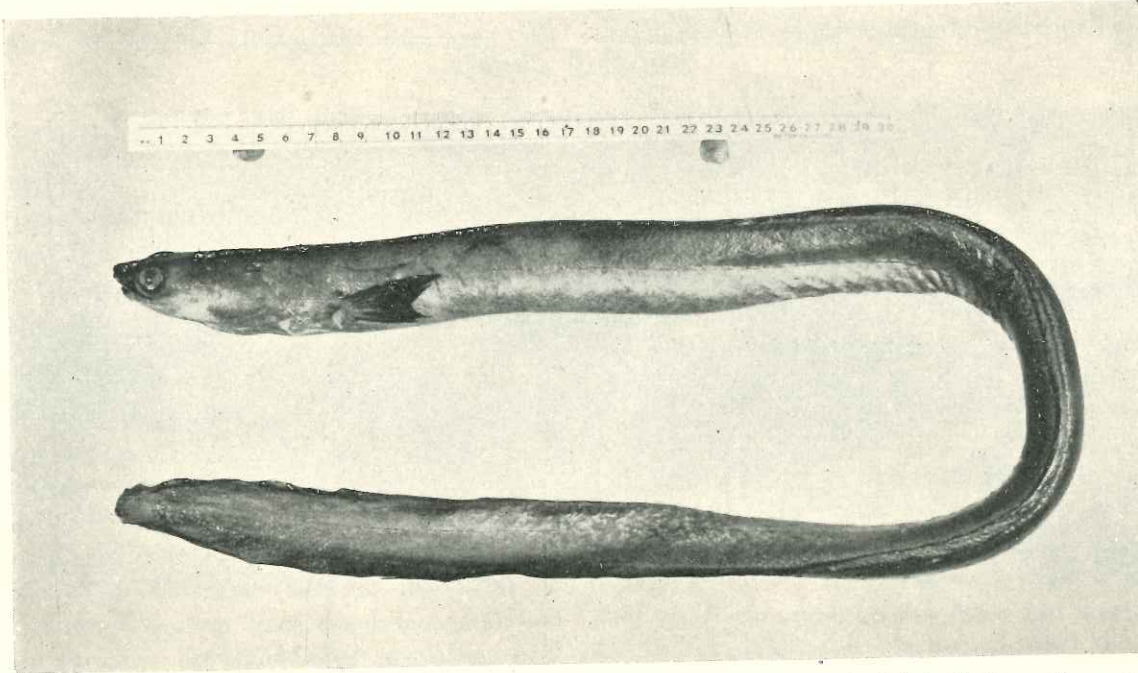


Fig. 2. Large-eyed female eel caught in the lake Furesø on August 19th, 1950 (phot. U. MØHL-HANSEN).

Storøjet hunål fanget i Furesøen den 19. august 1950.

present features that must be considered characteristic of the spawning dress of the eel.

Two quite corresponding Danish finds of female eels during recent years seem to indicate that these variants are not so very rare as would be supposed. The principal data of these eels are as follows.

1. Length 80 cm, weight about 500 g. Caught at Ballen on the east coast of Samsø about September 29th, 1946 (fig. 1).

The vertical and horizontal diameters of the eyes were 14 and 18 mm, respectively though this oval shape must be considered a consequence of the rather decomposed state in which the fish was received. The pectoral fins showed a black pigmentation, were pointed and had a length of 48—52 mm and a width of about  $\frac{1}{3}$  of the length.

On the arrival the skin showed a dark-brown

The eyes were large, circular and protruding, with a diameter of 13 mm.

The pectoral fins were long, black with a total length of 41 mm; both of them were bilobate.

The dorsal colour was brownish-grey, that of the sides above the lateral line bronzy while the ventral colour was silvery.

The width of the ovaries was 20 mm (fig. 3), the diameter of the eggs 0.2 mm.

A very characteristic feature in both eels was their famished state, which appears from a comparison of their weights with that of normal silver eels (abt. 800—1,000 g) of a corresponding length.

The large eyes, the prolonged and pointed, dark-coloured pectoral fins, the absence of fat and the more or less pronounced bronze coloration of venter and sides are no doubt characteristic of both sexes

of the eel at the spawning stage whereas the peculiar bilobate pectoral fins of eel no. 2 should probably be considered a deformity that is independent of these characters.

The question now is whether the essentially exterior, morphological changes that characterize these eels are the result of a natural development that would have ended in the maturation of eggs if the necessary external conditions had been present, or we have found a pathological state which, if so, must be supposed to have intensified those hormonal pro-

and gonads as is required for the accomplishment of the process of maturation.

In the said experiments with hormones the average egg diameters of up to 0.46 mm were developed without any considerable reduction of weight and without the far-going exterior morphological changes that characterize the eels described here in spite of the fact that the latter unquestionably represent a far more advanced stage of sexual development. It is perhaps legitimate to conclude from this fact that the hormones responsible for the two supposedly

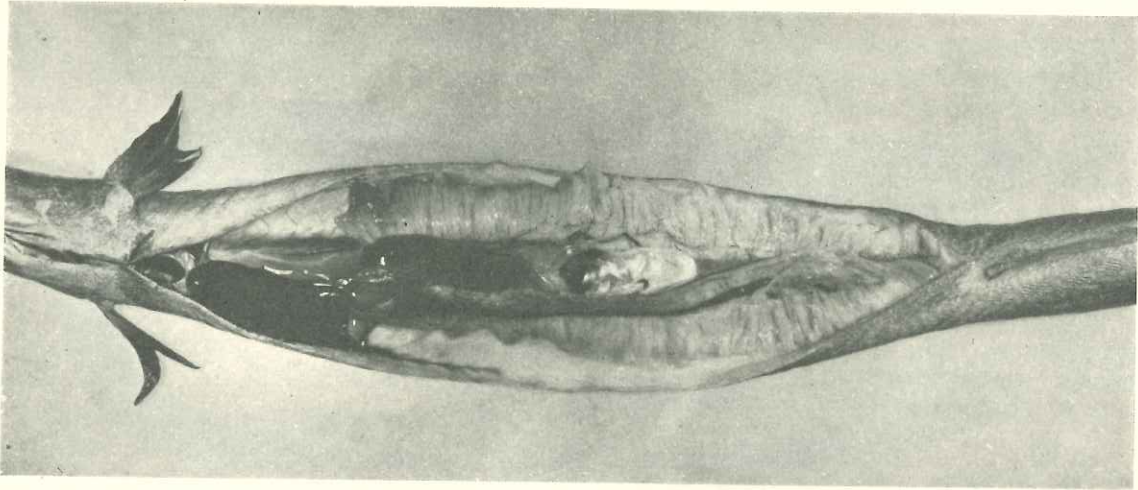


Fig. 3. The same cut open in order to show the sexual organs (phot. U. MØHL-HANSEN).

Samme opskåret for at vise kønsorganerne.

cesses, which otherwise do not result in the said changes that normally attend the maturation of the eggs until the fish is on its way across the Atlantic. The question cannot of course be safely answered as long as we have no material for comparison from the localities in which this stage of development is normal and not exceptional. We know that these exterior changes arise successively during the process of maturation, beginning with the growth of the eyes (cp. i. a. OTTERSTRØM, 1933), and that the process most likely ends in a total absence of fat and possibly in a partial decomposition of the musculature and the skeleton, as known for instance from the conger (*C. conger*). The total absence of fat at a stage when the eggs deviate inconsiderably in size from the eggs of normal silver eels seems to justify a doubt that these eels, assuming that the necessary external conditions were present, would be able to develop a further energy sufficient for such a growth of eggs

normally coincident processes of the maturation itself and of the exterior changes described here are not the same, and that the appearance of these characters consequently need not depend on a normal sexual development.

In this connexion it further seems reasonable to emphasize that eel no. 2 was hooked in spite of the fact that in its exterior it represents a further development of the silver eel stage, i. e. a stage at which the eel has already stopped feeding and the degeneration of the alimentary channel has started.

This fact seems to corroborate the opinion that the fish dealt with here are pathological variants although it is not unknown for other fishes, for instance the salmon, to be hooked at a time when otherwise no tasting of food takes place.

At present it seems legitimate to place these eels within the number of sexual variants of the vertebrates, the occurrence of which is due to a patho-

logically conditioned intensification of certain hormonal secretions with a subsequent shifting of the hormonal balance.

#### Litterature.

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### Dansk Resumé.

#### To danske fund af hunål (*Anguilla anguilla*) i hel eller delvis yngledragt.

Blankålene, der hovedsagelig om efteråret forlader de indvande og kyststrækninger, hvor opvæksten er sket, er endnu langt fra kønsmodenhed, og kun undtagelsesvis har man fundet blankål på et væsentlig mere fremskredent seksuelt udviklingsstadium end normalt. Særlig bemærkelsesværdig var en i 1903 i Præstø fjord fanget fuldmoden hanål, der foruden ved de stærkt udviklede kønsorganer indeholdende modne spermatozoer karakteriseredes ved meget store øjne og lange, næsten sorte, tilspidsede brystfinner.

Enkelte ål af begge køn med tilsvarende ydre morfologiske egenskaber som ålen fra Præstø fjord og yderligere karakteriseret ved en iøjnefaldende broncefaryng af bug og sider, for hunnernes vedkommende desuden i eet tilfælde ledsaget af en total mangel på fedt, er fra de sidste år kendt og beskrevet fra Sverige. Ingen af disse ål var dog kønsmodne.

To ganske tilsvarende hunål fanget her i landet omtales nærmere, idet der samtidig udtales den for-

modning, at disse varianter måske ikke er så sjældne, som man hidtil har haft grund til at antage.

De karakteristiske ydre forandringer hos disse ål, sammenholdt med ægudviklingen, der ikke er væsentlig mere fremskreden end hos almindelige blankål, rejser spørgsmålet, om ikke der er grund til at antage, at man står overfor en patologisk betinget aktivering af visse hormonprocesser, der ellers normalt må antages at ledsage ægmodningen.

Ud fra kendskabet til de ved behandling af blankål med kønshormoner opnåede resultater, der omfatter en ret væsentlig forøgelse af ægstørrelsen opnået uden tilsvarende dybtgående ydre morfologiske forandringer, som karakteriserer de her beskrevne ål, fremsættes yderligere den formodning, at det ikke er de samme hormoner, der er ansvarlige for de to processer, nemlig selve kønsmodningen og de formentlig normalt med denne sideløbende karakteristiske ydre forandringer.



**The Reports from the Danish Biological Station** (Nos. I—XXI) are published in the official Danish "Fiskeri-Beretning" for the years 1890—91 until 1912. After this year they appear as special publications. The Reports I—XXXII are edited by Dr. C. G. Joh. Petersen, the Reports XXXIII—XXXVI by Dr. A. C. Johansen and the later Reports by Dr. H. Blegvad.

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\*) The figures in ( ) refer to the "Fiskeri-Beretning" for the years quoted.

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