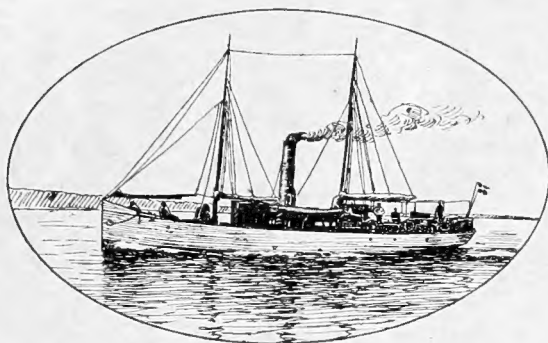


**Report**  
of  
**The Danish Biological Station**  
to  
**The Board of Agriculture.**



XX.

1911.

By

**C. G. Joh. Petersen,**

Ph. D.

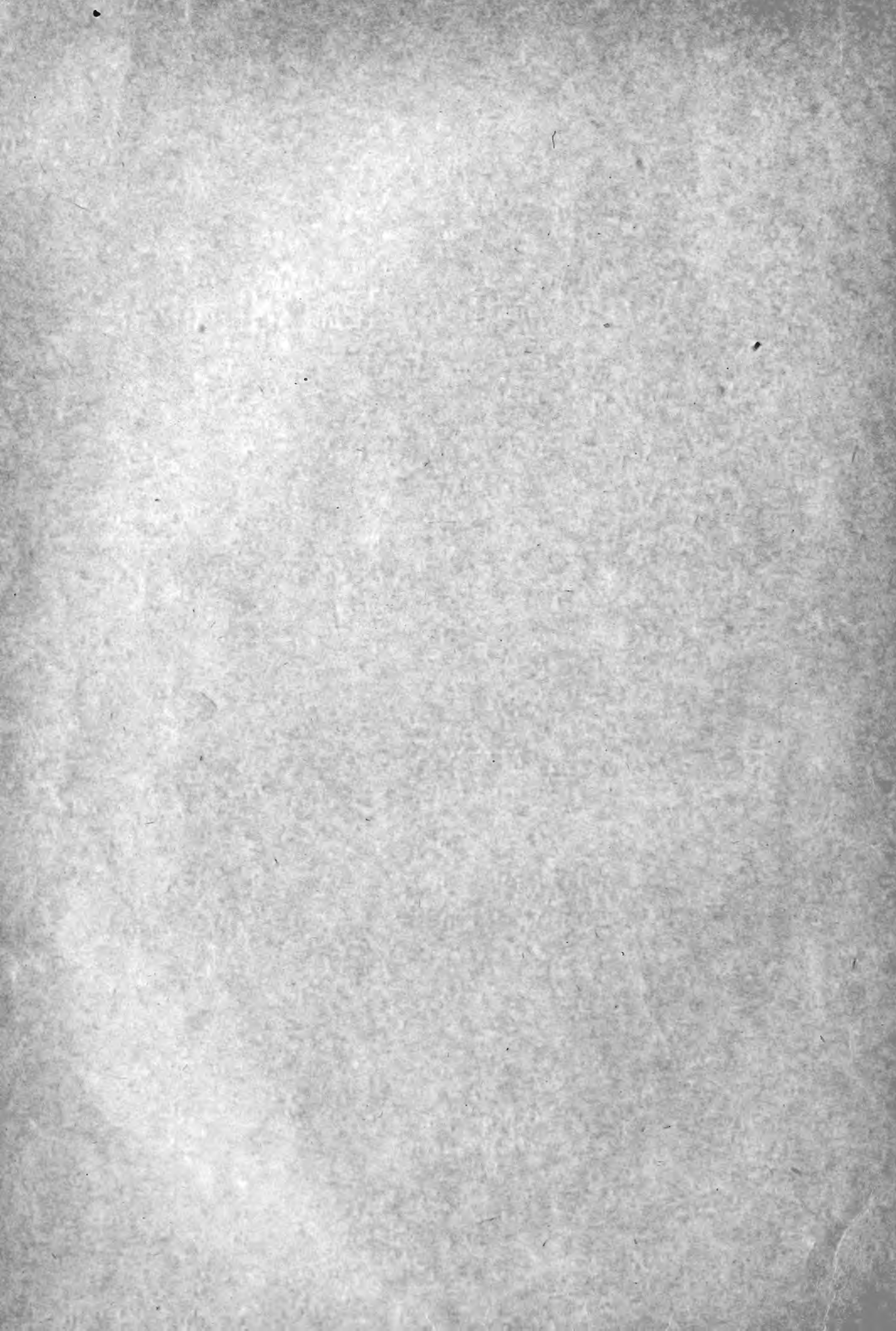
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Translated from „Fiskeri-Beretning for 1910“.

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Copenhagen.  
Centraltrykkeriet.  
1911.





From  
The Danish Biological Station.

XX

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1911.

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Copenhagen.  
Centraltrykkeriet.

1911.







# Valuation of the Sea.

## I.

### Animal Life of the Sea-Bottom, its food and quantity.

(Quantitative Studies.)

By

C. G. Joh. Petersen and P. Boysen Jensen.

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6 Tables, 3 Charts and 6 Plates.

#### I. Introduction.

Since 1883 I have been engaged in the study of the animal life of our Danish waters; it is only natural, therefore, that the ideas or conceptions, which at various times have formed the background for my studies, should gradually have altered to some extent.

In the first instance I endeavoured to obtain some insight into the occurrence of the single species of the bottom-fauna by means of a number of dredgings, especially in the Kattegat and Baltic; these investigations were carried out onboard the gunboat »Hauch« in the years 1883—87. The results are to be found in »Det videnskabelige Udbytte af Kanonbaaden »Hauchs« Togter«. 4<sup>o</sup>. 464 pages. (Atlas in folio.) 1893.

It was mainly an insight into the distribution of the invertebrates which was obtained, the larger fish could not be taken with the small apparatus used at that time; but the knowledge was gained from these investigations, that the occurrence of the lower animals is conditioned by certain laws, which produce an order and regularity specially evident in their bathymetric distribution. I endeavoured to show, that knowledge of the simplest natural conditions of the bottom and the waters could already for a great part explain many things and much in the occurrence of the animals («General Results») and from much later investigations in the same waters I have become convinced, that this order and regularity is not a phenomenon of short duration. The same characteristic occurrences are found again in the main after more than 20 years have passed, though I will by no means seek to deny, that a shifting, especially horizontally, does take place in the distribution of various species from year to year. The impression of the fauna as a whole remains however unchanged within such a short period of time as one generation. This holds good for the Kattegat and the Baltic, thus for comparatively open and large stretches of water.

In 1890 I began my work as Director of our »Biological Station», which was founded in that year, and investigations of a more purely ichthyological nature occupied my time for a number of years thereafter. From these investigations I learnt, among other things, that even though individuals of a species may occur in a water, that does not mean necessarily, that the species »belongs« there or can live the whole of its life there. Many fishes cannot reproduce in the enclosed waters, but nevertheless occur there year after year, either as young or on a longer or shorter visit; the eel, for example, is really only a guest in our waters, though it lives the greater part of its life here; it is »cradled« far away from our country. The plaice cannot spawn in our fjords but enters them in search of food. I saw that, to understand the distribution of the animals right to the bottom, we must study the occurrence of each species throughout the whole of its life. This has now been done for a number of fishes, though for only a few of the lower animals, and interesting information has in this way be gained. But even with all this we are not at the end of the requirements of biology with regard to the investigation of the animal life of the sea; the question of the food of the animals especially must naturally not be ignored. A good deal has also been written on this subject; long lists of what has been found in the stomachs of various fishes have been published and time and work have also been devoted to the study of the food of the lower animals, especially in recent years; but it does not seem to me, that we have yet got to the bottom in these matters.

The first time that questions of this kind came forcibly to my mind, was when I found, that the plaice in the western Limfjord ceased almost to grow for 2/3rds of the year, whilst those which were transplanted from these parts into the central Limfjord, increased their weight within the same time by 4 to 5 times what it was originally.

Many of the invertebrates on which the plaice feed are found at both places, so that I was obliged to believe, that it was the enormous abundance of the plaice in the western parts, producing the phenomenon I called »over-

population of plaice«, which alone was the cause of the slow growth there. This probably comes near to the kernel of the matter also, but there are perhaps other moments in addition. My first idea at that time was, that the slow growth might be due to the fact, that the bottom in the western parts out towards the North Sea was not so rich in food-animals as in the inner reaches; from this a new problem arose: how could we compare the quantity of the bottom-fauna at one place with the quantity at another?

In 1896, again with the help of the gunboat »Hauch«, I endeavoured to fish up all the animals on the bottom within a space of  $0.1 \text{ m}^2$ . by means of a somewhat primitive apparatus. The apparatus was fixed at the end of a long pole, long enough to reach the bottom in these shallow waters, which are only ca. 6—12 meters deep. A number of samples were counted, but the results have never been published. My impression, and also that of Dr. Th. Mortensen who assisted me at that time, was that there were almost as many animals in the western regions as in the inner fjord per  $\text{m}^2$ , and that the slow growth of the plaice in the west must therefore be explained from the principle of overcrowding. I shall return later to this question and only mention it here, because I believe, that it was the first time an actual counting of the animal life on the bottom per  $\text{m}^2$  was made, apart from a few attempts to count the quantity of the animals near the shore at ebb-tide.

It was in 1908 that I returned again to these investigations, as I now had a special steamer at my disposal and could carry them out better and in addition had found through numerous experiments a better apparatus, which could fish up the animals on  $0.1 \text{ m}^2$  even at considerable depths and without the pole. This apparatus, the » $0.1 \text{ m}^2$  bottom-sampler« has been much used during the 3 years 1908—9—10 and at many places in our waters; with its help we can quickly investigate whether a water is rich or poor in this or that kind of food, a matter that is of special importance with us, where the question of the implanting of plaice and flounder has become actual. Such an investigation is not possible with the dredge; I have seen how incorrect are the pictures we may obtain regarding the richness of the bottom from the use of the dredge. A certain comparison between two waters can certainly be obtained from the dredge, but this is not always sufficient, and it is especially impossible in this way to obtain a true measure of the quantity of food present, and as time went on I felt this to be more and more a necessity. It has now been proved over a number of years, that the transplantation of young plaice to the central parts of the Limfjord is a very profitable undertaking, even when only 40 or 60 plaice are transplanted per hectare, and the question thus arose, how many can be implanted per hectare before their growth becomes slow. In addition to being able to judge this matter simply by making a kind of artificial overcrowding, it would also be desirable, if we could estimate by some other way, by investigation of the quantity of the animals available as food, whether we were near or far from this danger-point.

The new bottom-sampler soon showed, that some of our waters are rich in animals which serve as food for the plaice, others poor, even exceedingly poor, and this was often accompanied by a different appear-

ance of the bottom-layers; the former had brown or gray deposits, the latter black and stinking. I therefore considered a more exact investigation of the deposits in our waters in high degree desirable, all the more as I have long known, that most of the lower animals in our fjords, which are not predatory or live on living plants, contained in their digestive tract a mass, which was nearly related or identical with the uppermost, brown layer covering the bottom of all our waters, where it is sufficiently deep and still for the fine particles to be deposited. I felt obliged to conclude, that this mass in the digestive tract of the animals composed their essential food and it was therefore of the greatest importance to know more precisely what its nature and origin was. This mass may be called dust-fine detritus; in addition to inorganic materials, it consists of a quantity of dead, deposited particles of plants and animals, among which we comparatively seldom find the remains of plankton organisms. »Living« microorganisms are naturally also found in the stomachs, but usually only in small quantity. We have so long and so often heard of the role the plankton is considered to play in the economy of the sea, that we almost forget the other sources of food, which however, at any rate in the smaller waters, certainly have an even greater importance. It seems to be time, therefore, that these sources were also investigated and estimated according to their value. An attempt in this direction will be made in the sequel. But just as the methods of plankton investigation have with time undergone extensive reforms, we may also expect, that our methods of investigation will become changed in much and many ways; what we report on here should rather be regarded as merely orientating investigations on an almost unworked field, where with new apparatus and new methods we have endeavoured to make a step forwards to an understanding of the metabolism of the sea, a subject first taken up by V. Hensen and later by K. Brandt in Kiel, but which none other, so far as I know, has attempted to carry further.

These investigations have cost much time and trouble, chiefly owing to the great amount of experimenting one way or another, and without my assistants Cand. H. Sell and Magister H. Blegvad, as also the crew of the »Saltingsund«, they would naturally not have been accomplished. In Dr. P. Boysen Jensen I have found one whose knowledge supplements mine in many directions; without his cooperation the matter would indeed not have been carried very far. Professor W. Johannsen has afforded me assistance in working up the numerical material and has placed the Plant-Physiological Laboratory of the University at our disposal for making the necessary analyses, for all of which we owe him special thanks. The scientists of the Zoological Museum of the University have also assisted us in the determination of various animal forms and I would especially thank Professor H. Jungersen, Dr. Th. Mortensen and Docent Stamm for their cooperation.

The sections II—IV have been written by Boysen Jensen, the rest by C. G. Joh. Petersen.

Copenhagen, 12. February 1911.

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## II. Sources for the organic matter in the sea.

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Just as on the dry land, the lifeless organic matter in the sea must in the first instance originate from living, carbon dioxide assimilating plants, since as known it is only through their agency, that the inorganic materials in nature, particularly carbonic acid, are transformed to organic substances.

On close examination we may divide the organic matter in the sea into 3 groups according to the place where they are produced.

1. The organic matter produced in the sea itself.
2. The organic matter brought down by rivers and streams.
3. Organic matter carried out from the land into the sea by the agency of the wind.

For a quantitative consideration it is evident that the last source is of no importance, in comparison at any rate with the first two; but without committing any great error we can also eliminate the second source, so far as the waters are concerned with which these investigations chiefly deal. As is known, there is only one river of any size which flows out into the Limfjord, namely, the Karup River which runs out into Skivefjord. We cannot say how large are the quantities of organic materials which this river carries down, but we may certainly assume that these materials are deposited in Skivefjord and are of no importance for the rest of the Limfjord.

There only remains for consideration the materials produced in the sea itself, in other words, the vegetation of the sea.

A review of the plant-formations occurring in water is given by Warming: *Oecology of plants*, 1909, p. 155 *et seq.* Taking account only of the autophytic formations which occur in salt water, we obtain from this review the following subdivisions of the vegetation in the sea.

- I. Free-floating or free-swimming plants:
  - The plankton formation.
- II. Fixed plants (benthos formation):
  - A. Fixed to stones or rocks:
    - The marine algae formation.
  - B. Fixed to loose soil:
    - Grass-wrack formation.

Again, the saltwater plankton (haloplankton) is subdivided into oceanic and neritic plankton, according as it occurs out in the open sea or at the coasts. The principal forms of the plants occurring in the plankton are various diatoms (*Chatoceros*, *Rhizosolenia* etc.), *Peridineae*, *Flagellata* etc.

In contrast to the plankton, the benthos formations are bound to the coasts. The marine algae grow most luxuriously on rocky coasts, e. g. the coasts of Norway, of Great Britain, the Færoes and Iceland. Darwin's description of the algal forests on the coasts of Patagonia is well-known. In their wealth and extent he compares them to the primeval woods of the tropics. The brown algae are predominant, in southern seas for example *Macrocystis* and *Sargassum*, in northern seas various species of *Laminaria*, *Fucaceae* and many more. The

grass-wrack formation is formed chiefly of various plants of the family of *Potamogetonaceae*, *Zostera*, *Ruppia*, *Zannichellia*, *Cymodocea*, *Posidonia* etc.

After this brief summary we may turn to the vegetation in the Danish waters, especially the Limfjord, and begin with a consideration of the benthos formations, which are mainly represented by the grass-wrack formation.

*Zostera marina* is everywhere the predominant plant. It extends in a more or less broad, broken belt along all our Kattegat and Baltic coasts, occurring in patches over a great part of the Kattegat and in great quantities in all our fjords.

The occurrence and biological conditions of the *Zostera* have been described in the following papers:

1. »Det videnskabelige Udbytte af Kanonbaaden Hauchs Togter« by C. G. Joh. Petersen, 1883—1886.
2. C. G. Joh. Petersen: »Fiskenes biologiske Forhold i Holbæk Fjord«. Ber. fra den Danske biologiske Stat. I. 1890-(91).
3. C. G. Joh. Petersen: »Det pelagiske Liv i Fænø Sund«. Ber. f. D. biol. Stat. III. 1893.
4. Warming: Dansk Plantevækst I. Strandvegetation. 1906.
5. Ostenfeld: Aalegræssets (*Zostera marinas*) Vækstforhold og Udbredelse i vore Farvande. Ber. f. D. biol. Stat. XVI. 1908.

I shall only give a short summary here of the results obtained by these investigations, chiefly on the basis of Ostenfeld's work.

*Zostera* grows best in a salinity of 1—3‰, but can also grow in water of less salinity. The situation must be somewhat sheltered. In the North Sea, therefore, it only occurs in small quantity. The depths to which it descends are the following:

In the Limfjord ca. 6 meters.

In the Kattegat (Aalborg Bugt) ca. 11 meters.

In the Baltic (Fakse Bugt) ca. 8 meters.

In Guldborgsund and Faenø Sund ca. 6 meters.

The *Zostera* thus goes furthest out where the water is clearest. The nature of the bottom is also of importance for the *Zostera*. The *Zostera* which occurs on solid ground is shorter and narrower leaved than the fjord *Zostera*, which grows on muddy bottom.

The distribution and occurrence of the *Zostera* is illustrated by Chart II in »Hauchs Togter« (Kattegat), by the Charts on pp. 17 and 29 in Ostenfeld's work (Limfjord and Kattegat). Further, Charts showing the distribution of the *Zostera* in Holbæk Fjord and the Little Belt are given in Ber. f. D. biol. Stat. I and III.

Briefly, the distribution of the *Zostera* is the following (from Ostenfeld l. c.):

In the North Sea the *Zostera* is known from the waters between Fænø and the mainland and further from Hobugt. On the other hand, it is absent or occurs very sparsely at least along the whole of the west coast of Jutland.

In the Limfjord, on the other hand, the *Zostera* vegetation is extremely rich and luxuriant. It follows fairly closely the 6 meter line, occurring therefore in greatest quantities in the shallow Brednings, Venø Bugt, in Skibsted Fjord,

round Agerø, in Louns Bredning, Skivefjord, in the waters between Logstor and Nibe. In Thisted and Livø Brednings, where the shores slope down fairly steeply, it only occurs as a narrow belt along the coast.

In our other fjords also, in the East Jutland fjords, in Odense Fjord, in Roskilde and Holbæk Fjords, the *Zostera* vegetation occurs extensively and luxuriantly.

In the Kattegat there is a belt of (narrow-leaved) *Zostera* along the east coast of Jutland. In patches it occurs over great parts of the Kattegat, especially south of Læsø and in Samsø Belt, but, as a glance at the Charts quickly shows, the Kattegat vegetation in comparison to the extent of the water, is many times less than that of the Limfjord; it is also, as above-mentioned, less luxurious than the fjord *Zostera*.

In addition, some other flowering plants belong to the grass-wrack formation as well as *Zostera*, the most important of which are *Zostera nana*, *Ruppia maritima* and *Potamogeton pectinatus* (see Warming, 1906, p. 185 and Ostenfeld 1908 p. 38). In comparison with the *Zostera* they play quite a subordinate role, occurring more seldom and forming only small growths. Most important are *Ruppia* and *Potamogeton*.

More important than these in quantitative regards is probably the epiphytic algal vegetation, which grows on the *Zostera* leaves (Ostenfeld, 1908, p. 32). The leaves of the fjord *Zostera* are often quite laden with short brown and red algae (Ostenfeld calls them *Ceramium* and *Ectocarpus* species). Further thick mattings of diatoms occur. The whole of this epiphytic flora constitutes the food for a rich fauna, which likewise lives on the *Zostera* leaves, various gastropods (*Rissoa*, *Hydrobia*), *Bryozoa* etc. (see figure in Ostenfeld l. c. p. 33). This fauna will be discussed in more detail later.

The marine algae formation is also represented in the Danish waters. Round about the *Zostera* belt, both within and outside, numerous stones are of frequent occurrence and thus offer possibilities for the growth of marine algae. Ostenfeld (l. c., p. 32), distinguishes between pure and mixed *Zostera* vegetations. The pure *Zostera* vegetation occurs on soft muddy soil; at such places it is the only plant occurring except for the above-mentioned epiphytic algal vegetation. Marine algae are not able to grow at such places, partly because there are no stones and partly because the *Zostera* is able to smother them by excluding the light. In shallower water, on the other hand, and on solid bottom on the whole where stones occur and where the *Zostera* as mentioned grows less luxuriantly, a rich algal vegetation develops at certain places. Regarding the production of the marine algae in our waters Dr. Kolderup Rosenvinge has most kindly written a brief account, which may be given here.

»If we wish to determine the total, annual production of matter by the algal vegetation in the Danish waters, we may for the few most important species endeavour to find out, how much new material is formed each year and on the other hand, how much dies or is thrown off.

To be able to make such an investigation some of the species must first

be indicated which play the principal part in the composition of the vegetation, namely the following:

*Fucus serratus*,  
*Fucus vesiculosus*,  
*Laminaria* (not in the Limfjord and other fjords),  
*Halidrys siliquosa* (rare in Limfjord),  
*Furcellaria fastigiata* (and *Polyides rotundus*),  
*Chorda Filum*,  
*Phyllophora membranifolia* and *Ph. Brodiaei*,  
 Fine, bushy *Florideae* (*Polysiphonia* species, *Rhodomela subfusca*, *Ceramium* species, *Cystoclonium purpurascens*, *Brongniartella byssoides*).  
*Delesseria* species (not in Limfjord),  
*Desmarestia aculeata*,  
*Cladophora gracilis* (especially in fjords),  
*Ectocarpus* species.

These algae are normally attached, usually to stones or on other algae, but also to Mollusc shells, *Zostera* and the like. Some of them are annuals, the individuals dying off completely, as a rule in the autumn or winter. This is the case with *Chorda Filum*, and it also holds good for several of the finer, bushy *Florideae* (*Polysiphonia* and *Ceramium* species) and *Ectocarpus* species. Others do not die down quite completely, there remains a small basal part from which new shoots spring up in the following year (*Cystoclonium purpurascens*, *Brongniartella*, and several others not mentioned here, which however may be of no little importance, especially in the littoral zone); the hibernating part is however so small in comparison with the part that dies down, that these species may for practical purposes be placed in the same class with those which are really annuals.

The most of the above-mentioned algae are however perennial, so that they are to be found at all seasons of the year with a complete complement of all essential parts of the leaf; in these also, nevertheless, a greater or smaller part of the leaf is thrown off annually. How large is the part cast off in this way, is in most cases very difficult to say. In *Laminaria* it is easy enough, as the leaf is changed every year, whilst the stalk remains, and the leaf contains several times more substance than the stalk. In others it is more difficult, and in any case the matter has not been closely investigated, but so much at any rate can be said, that the fruit-bearing parts, i. e. the parts which contain or directly bear the reproductive organs, die after these have been emptied. These parts in some are very large in proportion to the total mass, more than half of the shoots in question, e. g. in *Furcellaria*. In others the fruit-bearing parts are but small in comparison with the total mass, as in the *Fucus* species, *Halidrys*, *Ascophyllum*; but in these not only are the fruit-bearing parts thrown off, but also larger or smaller parts of the fruit-bearing shoots. How much this amounts to cannot be said with certainty, as it is certainly different for the separate species and for these in different localities, and for individuals of different ages. In some of these species the annual growth will perhaps not amount to the half part, in others it will probably exceed this.

That the annual production of substance is on an average very considerable,



is a fact which has strongly impressed me from dredgings made in the month of January (in the Great Belt and Northern Kattegat). The total mass of algae I obtained in the dredge was generally much smaller than in the summer, and I received from this the definite impression, that the annual production of substance is much more than the half part of the mass which is found in the most luxuriant period of the year (early summer).

In addition to the parts which fall off owing to age, an enormously large quantity of parts and whole plants are broken off by outer mechanical forces (waves, currents, fishing apparatus). Many of these soon die, but some are able to retain vitality, in some cases for years, as they continue to grow whilst dying off below. This is what occurs especially in *Furcellaria* and *Phyllophora Brodiaei* on soft bottom-soil in the fjords and other sheltered places. The yearly increment of these two algae in the loose condition is perhaps less than half of the substance present at a definite point of time, as one can often recognize more than two generations of shoots on them; yet it must not be forgotten, that the greater number of shoot-generations is possibly counterbalanced by the large amount of branching, especially in *Furcellaria*, which results in most shoots in the last generation and in certainly many individuals dying, partly of old age partly because they come under unfavourable conditions. So long as definite investigations are wanting, it is not possible to say with any certainty how great the annual production of substance is in the loose algae, but I do not doubt that the annual production in the marine algae, even including the loose algae, is more than the half, and probably much more than the half of the algal mass present at any time.

With regard to the *Zostera* (grass-wrack), reference may be made to Ostensfeld's report in the XVIth Report from the Danish Biological Station, 1908. He did not come to any decisive result, it is true, but he suggests, that 4 to 6 new leaves are produced annually on each shoot. As the number of leaves according to his tables varies between 4 and 7, it seems that the leaves entirely or for the most part are renewed in the course of one year. To this we must add, that a large part of the older plants produce long, flowering shoots, which are entirely thrown off after the ripening of the fruit. With regard to the annual production of substance the *Zostera* vegetation can thus be compared with a permanent grass-field on land.

If we were to compare the algae-covered stretches of the sea-bottom with plant formations on land, with regard to the amount of production, the comparison should rather be with pasture land covered with herbaceous plants, including various annuals, but also many shrubs and some low bushes.\*

With this we may conclude our review of the benthos formations in the Danish waters. As we have seen, the *Zostera* plays the most important role.

We may now consider

#### The Plankton formation.

Regarding the plankton in the Danish waters we also find information in the Reports from the Danish Biological Station (C. G. Joh. Petersen: Plankton-Studier i Limfjorden, Beretn. f. d. d. biol. Stat. 1897, as also De danske Farvandes Plankton i Aarene 1898—1901, K. D. Vidensk. S. Skr. 6 R. XII, 3). In 1896

and 1897 Petersen took 3 series of plankton samples, beginning in the North Sea and extending through the Limfjord and out into the Kattegat, in one case right down into the Baltic. The plankton samples were taken with Hensen's quantitative net. The quantity of plankton was determined, partly from its volume and partly from its weight. It appears from these investigations, that the North Sea is poor in plankton in comparison with the Limfjord and the Kattegat. The Limfjord at certain times of the year is rich in plankton organisms, chiefly diatoms. Two plankton maxima occur, one in the spring and one in the autumn. The diatom plankton arises in the Limfjord itself and does not enter from outside. I shall return later to these plankton investigations.

The sources for the organic materials in the sea are mainly the vegetation there. The vegetation in the sea falls again into two divisions, the vegetation of the *Zostera* region and the plankton organisms. The question is now, whether these two groups are of equal importance in quantitative regards, or whether one of them plays the predominant role as source for the organic matter and as food for the animal world of the sea. To this question, **the vegetation of the *Zostera* belt or the plankton organisms**, we shall endeavour to give an answer in the following chapter.

### III. Deposits of organic matter on the sea-bottom.

**1. Introduction.** The organic matter produced by the plants is at last, in so far as it is not previously destroyed, deposited on the sea-bottom. Late in the autumn the *Zostera* leaf-blades are thrown off, whilst the leaf-stalk, as Ostensfeld has explained, remains. The loosened leaves drift about for some time on the surface of the water, supported by the air-vesicles the *Zostera* leaves contain. At last they sink to the bottom and remain sometimes in quiet localities, in inlets, channels and the like, as the »dead-weed«. More frequently, however, the *Zostera* leaves are torn in two, partly mechanically, partly by the destructive agency of various bacteria, and are scattered over the sea-bottom in the form of small, more or less unrecognizable particles. The algae, so far as they are attached, are also torn loose and carried away from the place where they grow. They do not contain air-vesicles like the *Zostera* (with exception of *Fucus* and *Halidrys*) and they are not met with therefore floating on the surface. The plankton organisms also, in so far as they are not destroyed, must end on the bottom.

It is thus characteristic of the metabolism of the sea, that the organic materials do not remain at the place where they were produced but are distributed more or less uniformly over large areas. It is easy to see that this condition has quite a supreme importance. As mentioned in the previous chapter, the vegetation in the sea (apart from the plankton) is greatly localised in contrast to the vegetation on land, as only an inappreciable part of

the sea-bottom bears vegetation. If the above-indicated distribution of the organic materials did not take place, therefore, the greater part of the bottom of the sea would be bare, not only of vegetation but also of the animal life dependent on the vegetation. The latter, as will be shown, has in fact its basis in the organic matter originating from the *Zostera* belt.

In the deposits on the sea-bottom we almost always find therefore larger or smaller quantities of organic materials. The distribution, origin and conditions of deposition of this organic matter will be more closely discussed in the sequel.

**2. Historical summary.** We may first consider the works which have dealt with the nature of the sea-bottom, and we must first mention the »Challenger« Expedition (Report of the scientific results of the voyage of H. M. S. »Challenger« 1873—76). On this Expedition a very large material was collected, which has been worked up and published by Wyville Thomson and John Murray: »Deep-sea deposits«. From this extensive work we cite only a single passage, concerning albuminoid and other organic matters in deep-sea deposits: »In the Red Clays and the other truly pelagic deposits the organic matter is much less« than in close to the shores. Quantitative determinations of the amount of organic matter in the bottom samples were not made.

These were not made either with the bottom samples collected by the »Ingolf Expedition« and which were worked up by Bøggild: »Havbundens Aflejring« (Den danske Ingolfekspedition I, 3).

On the other hand, we know more about the deposits of organic material in freshwater, in Denmark through Wesenberg-Lund's excellent investigations in our freshwaters. (Studier over Søkalk, Bønnemalm og Søgytje, Medd. f. D. geologisk Forening Nr. 7). According to these investigations a very considerable amount of organic material is deposited on the bottom of our deeper lakes, affording food for a rich animal life, which exists on the bottom of the lakes. The bottom-soil is passed through animals in this way and thus a bottom deposit is formed, which in accordance with v. Post is called by the name gytje, by which is understood »the bottom deposits formed in pure clean water chiefly by the excremental agency of the bottom-fauna«. According to Wesenberg-Lund the organic parts of the lake-gytje arise either from the neighbouring land's plant and animal world, from the littoral zone of the lake or from plankton. In the different lakes these sources are of somewhat different importance. In the case of the plankton the results are stated as follows: »In the larger and deeper lakes the soft parts are dissolved before the plankton sinks to the bottom, so that it is only deposited in the form of skeletal parts. In shallow lakes on the other hand the soft parts of the plankton also enter into the composition of the gytje.

**3. Methods for the study of the sea-bottom.** To obtain samples of the sea-bottom two apparatus have been used, the  $0,1 \text{ m}^2$  bottom-sampler constructed by C. G. Joh. Petersen to be described later (see Chap. VI). I need only remark here, that with the help of this apparatus we obtain a piece of the bottom  $\frac{1}{10}$ th of a  $\text{m}^2$  in its natural position, without the separate layers being mixed. Thus we are able on the one hand to subject the sea-bottom to a macroscopic and microscopic examination, and on the other to take out samples for further analysis of the surface or underlying layers, just as we may wish. The second apparatus,

also constructed by Petersen, consists of a thick-walled glass-tube with a lumen of ca. 1 cm., a thickness of 1–2 mm. and a length of 50–55 cm. The upper end of the glass-tube is attached to a lead. When it is sunk down the glass-tube penetrates some way into the bottom and takes up a cylindrical plug of the bottom-material. Such a bottom-sample gives especially an excellent picture of the arrangement of layers in the sea-bottom. If we wish to examine the single layers more closely, possibly under the microscope, the end of the cork is cut away below and the remainder is pushed up the tube with the bottom-sample, and the latter as it comes out of the tube can be examined for every depth. These glass-tubes are naturally only suitable for soft bottom; hard ground they cannot penetrate. On muddy bottom the adhesion of the bottom-sample to the sides of the glass is sometimes so small, that the sample slides out when the glass tube is being hauled up through the water. In such cases frequently the end is achieved by using narrower tubes. In too deep water, probably, it will not be possible to use these tubes.

**4. Sea-bottom in Thisted Bredning.** In describing the sea-bottom in the Limfjord we may begin with that in Thisted Bredning, which in many ways may be taken as to a great extent typical of the great part of the Limfjord. A bottom-sample from the deep part of the Bredning, taken with the above-mentioned glass-tubes, will show us the following: uppermost we have a very characteristic layer of 1–2 mm. in thickness. From its colour we may call it the brown layer. It consists of fine particles, which lie very loosely together, so that the surface has a fluffy appearance. Seen under the microscope this uppermost layer is found to consist of numerous particles, for the most part indeterminable as to origin. In addition to inorganic materials, particles of clay and the like, we find all sorts of other things, e. g. chitin needles, a few shells of diatoms and fairly frequently larger things, which are distinctly seen to consist of the tissues of higher plants.

In order to determine the nature of the organic components occurring in the sea-bottom, I made some micro chemical analyses on a dried sample of the uppermost layer in Thisted Bredning. One might be inclined to expect some quantity of cellulose, but this was not the case. Only very few of the particles of the bottom were coloured blue with chlor-zinc-iodine; the greater part remained either colourless or assumed a brownish colour. On the other hand, Ruthenium-red, which as known gives a reaction with pectoses, coloured many of the particles intensely red.

In the brown layer here and there we find some small, spindle-shaped, brown balls, which fairly easily suffer compression under the cover-glass, and which are undoubtedly excrements, probably of Lamellibranchs.

Of living organisms, apart from bacteria and higher animals, there are but few; one or two living bottom diatoms are met with.

Under the brown layer we find a layer of dark-blue colour, extending to the bottom of the sample and consisting of sand-mixed clay with organic remains.

The whole of the bottom-sample is free of smell.

A bottom of this kind covers the whole of Thisted Bredning outside the 6 meter line. Inside the 6 meter line we have the *Zostera* belt and inside this

again a belt of sand. In Thisted Bredning both of these belts are as a rule very narrow.

The question is now, what we should call a bottom deposit of this kind. As mentioned above, the name *gytje* is used to indicate certain freshwater deposits, which are rich in organic material and which have arisen by the excremental agency of the bottom-fauna. It does not seem to me that this name can be used for a bottom-deposit of the above-described nature. In this the quantity of excrement plays far too small a role. The main quantity of the organic material found in the brown layer has scarcely passed through any digestive tract and will scarcely do so. Mixed with inorganic materials, sand and clay, it will gradually sink down into the underlying, black-blue layer, without ever being excrement.

On the whole it does not seem to me possible to find a common name for such a heterogeneous mixture as is found in the bottom-soil of Thisted Bredning. There is also the difficulty that a bottom-deposit of this kind passes over in other parts of the Limfjord without boundary into bottom-deposits of a similar character, but of somewhat different composition. It is common to probably all the bottom soils in the Limfjord, that they consist of an intimate mixture of sand, clay and organic materials, but these components are present in extremely different quantities. If the quantity of the organic material grows greatly, as is the case in many of the inner reaches, Louns Bredning, Skivefjord etc., we obtain bottom-deposits which resemble those we commonly call mire or mud, and as the quantity of organic material and clay decreases, we obtain almost pure, sandy deposits, e. g. at several places in Nissum Bredning. I am thus inclined to think, that the bottom-deposits in the Limfjord should not be characterized by names but by analyses. And the characteristics, which should be of the greatest importance here, are the quantity of organic material, clay and sand and carbonate of lime. In the following section a series of bottom-samples from different Danish waters will be discussed. At present I have only made determinations of the organic material they contain.

**5. Investigation of bottom-samples from Danish waters.** The bottom-samples used in these investigations were taken with the 0.1 m<sup>2</sup> bottom-sampler. When the bottom-sampler was opened and the bottom-sample lay in its natural position on the deck, the sample for analysis was selected with a small spatula at right angles to the surface of the sample and to a depth of ca. 3 cm. Altogether ca. 100 gm. were taken, brought into a glass and covered with alcohol, the whole being then well shaken. On returning to Copenhagen the bottom-samples were dried at 60°—70°, then pulverised in a mortar and again dried at 100°.

In the material thus obtained the quantity of carbon was determined according to the method given by Kjeldahl (Medd. f. Carlsb. Laborat. III p. 110, 1891). The principle of the method is to convert the carbon to carbon dioxide by means of concentrated sulphuric acid and bichromate of potassium, and then absorb and weigh the carbon dioxide formed. The splitting up was made in a long-necked retort with a volume of 100 cm<sup>3</sup>. The retort was provided with an india-rubber cork with double bore for the inlet and outlet tubes, of which the inlet tube went right to the bottom of the retort. By means of an air-pump a

stream of air could thus be sent through the retort in order to take up the carbon dioxide and lead it over into the absorption tubes. A wash-bottle was inserted before the retort and filled with soda-lime to cleanse the stream of air of carbon dioxide. From the retort the stream of air passed through a U tube in an asbestos-covered oven; this tube contained granulated copper dioxide (after Messinger, Kjeldahl uses here dioxide of mercury). The object of this copper dioxide, which is greatly heated up during the separation, is to oxidize certain products which are not completely oxidized to carbon dioxide in the retort. Behind the oven is inserted a wash-bottle with concentrated sulphuric acid to dry the stream of air, which then passes through two weighed U tubes with sodium carbonate which takes up the formed carbon dioxide in the stream of air.

The separation was made with an addition of 10 gm. of bichromate of potassium and 30 cm.<sup>3</sup> concentrated sulphuric acid to the substance. The whole was heated up slightly until gas was given off. The duration of the analysis was 1½ hours.

Before the quantity of carbon is determined, all the carbon dioxide from carbonates must naturally be removed first of all. This is done by covering the weighed substance with a strong solution of phosphoric acid and letting it dry at 60°—70°.

From the found quantity of carbon dioxide the quantity of carbon is calculated and this is again calculated in percentage of the bottom-sample in dry condition.

To test with what degree of accuracy the determination of carbon could be made by this method, I weighed 251 mgm. of pure cane-sugar, which according to calculation should yield 387 mgm. carbon dioxide; 365 mgm. carbonic acid was obtained, thus ca. 5 % too little. When we remember that it is the relative and not so much the absolute values we want in these investigations, an error of this dimension cannot be said to have any importance.

The determination of the nitrogen was made according to Kjeldahl's method.

The result of the analyses was as follows:

1. North Sea, 3 miles west of Agger; depth 16 meters. Two bottom-samples were taken, the one consisting of fairly pure sand, the other with somewhat more clay. Equal parts of the samples were mixed together. This sample contained 0.34 % C and 0.027 % N. The quotient  $\frac{C}{N} = 12.6$ .

2. Nissum Bredning, off Røiensø Odde; depth 6 meters. The bottom-sample contained a good deal of sand. It consisted of 0.58 % C and 0.045 % N. The quotient  $\frac{C}{N} = 12.4$ .

3. Kaas Bredning. The bottom in Kaas Bredning greatly resembles the bottom in Thisted Bredning, which was described in detail above. The bottom-sample used for analysis was taken in the middle of the Bredning in 6 meters depth. It contained 1.58 % C and 0.142 % N. The quotient  $\frac{C}{N} = 11.2$ .

4. Kaas Bredning. Another bottom-sample was taken in Kaas Bredning off Kaas Hoved at 11 meters depth. As was to be expected, this sample contained a little more carbon than sample 3, namely 1.98 %.

5. Vilsund. The bottom-sample consisted of dark mud, with remains of *Zostera*, depth 14 meters. The carbon amounted to 2.07 %.

6. Thisted Bredning, Sennels Church in N., 2 miles from land, depth 8 $\frac{1}{4}$  meters. The bottom-sample contained 1.01 % C.

7. Thisted Bredning; Hanklit in S. W. by S., 1 $\frac{1}{2}$  miles from land. The bottom-sample was characteristic for Thisted Bredning. The depth was 10 meters. The sample contained 1.77 % C and 0.166 % N. The quotient  $\frac{C}{N} = 10.6$ .

8. Thisted Bredning. Same place as sample 7. The uppermost, brown layer was scraped off and analysed. It contained 3.06 % C, thus more organic material than the bottom-sample as a whole.

9. Louns Bredning. The bottom in Louns Bredning consists of black, somewhat stinking mud. The bottom-sample was taken off Louns Church, N  $\frac{1}{2}$  W, 1 $\frac{1}{2}$  miles from land. Depth 6 meters. The sample contained 4.3 % C and 0.374 % N. The quotient  $\frac{C}{N} = 11.5$ .

10. Directly off Glyngøre. The bottom-sample was taken in the deep channel off Glyngøre at a depth of 21 meters. The bottom consists of black, stinking mud with many remains of *Zostera*. The sample contained 4.05 % C.

11. West of Furhoved. The bottom greatly resembled that in Thisted Bredning; it was quite without smell. The depth was 8 meters. The sample contained 2.24 % C.

12. Off Blødens Pæle (in the eastern part of the Limfjord in the neighbourhood of Hals). Depth 13 meters. The bottom consisted of black, stinking mud with a thin, brown layer, containing many living diatoms. The bottom-sample contained 1.12 % C and 0.138 % N. The quotient  $\frac{C}{N} = 8.1$ .

The following bottom-analyses came from the Isefjord.

13. Roskilde Bredning. The bottom here is of quite a characteristic nature. It consists of a uniform, black, stinking mud, which quivers like a jelly. This layer of mud is very thick; a pole could be inserted several meters down. Just as in Thisted Bredning a very thin, brown layer lies above the mud. When such a mud sample is dried, it shrinks considerably; it contained, when tested, no less than 85 % of water (for the sake of comparison, it may be mentioned that a bottom-sample from clay bottom in the Kattegat contained ca. 62 % water). The bottom-sample which was taken at a depth of 3.5 meters, contained 10.2 % C; this is the largest quantity of carbon I have ever obtained. On adding hydrochloric acid to the bottom-sample, hydrogen sulphide was given off. We shall return later to this point.

14. Isefjords large Bredning. The bottom here is much lighter than in Roskilde Bredning, with a greenish yellow colour, but curiously enough it has the same quivering consistency as that in Roskilde Bredning, though somewhat less marked. The bottom-sample, which was taken at 9—10 meters depth, contained 2.27 % C.

15. Bramsnæs vig. The bottom is of similar nature to that in Roskilde Bredning, but not quite so black. It contained 8.6 % C.

Lastly, we have a few bottom-analyses from the Kattegat.

16. Anholt; depth 34 meters. The bottom-sample consisted of fine clay

without the brown layer so characteristic of many of the above mentioned samples. The sample contained 2.36 % C and 0.204 % N. The quotient  $\frac{C}{N} = 11.5$ .

17. W. N. W. of Kullen; depth 30—35 meters. The bottom consisted of fine, gray clay and contain 2.29 % C.

18. S. S. E. of Sprogø; depth 20—25 meters. The bottom consisted of fine sand, with a thin, brownish gray layer, and contained 2.15 % C.

In order, further, to compare the bottom in our home waters with the sea-bottom at greater depths, some determinations were made of the organic matter in bottom-samples, which were taken by the second Ingolf Expedition, and which the Zoological Museum kindly placed at my disposal. These bottom-samples were taken with Baillie tubes, which take up a cylindrical plug of bottom-soil quite like the above-described glass-tubes. Immediately on being taken up the samples were covered with alcohol and shaken. To carry out the carbon determinations I dried a small part of the samples in the manner described above. The analyses apply to the bottom-soil from the surface down to a depth somewhat different for the various stations. The length of the plug taken up by the Baillie tube is, namely, very different according to the nature of the bottom.

We may begin with 3 stations lying south of the Ridge which runs from the Faeroes over Iceland to Greenland. The bottom-temperature was positive.

Station 45. 61° 32' N. L., 9° 43' W. L., depth 643 fm., bottom-temp. 4.17°. The bottom-sample was characterized by Bøggild in the following manner (Havbundens Aflejringer. Den danske Ingolf-Ekspedition 1. 3): Globigerina clay, in moist condition: light, brownish gray, coarse sandy clay; in dried condition: light brownish gray, somewhat strongly coherent. 47.02 % Ca CO<sub>3</sub>.

The bottom-sample contained 0.41 % carbon.

Station 46. 61° 32' N. L., 11° 36' W. L., depth 720 fm., bottom-temp. 2.4°. Bøggild: Transition-clay, in moist condition: brownish gray, fine clay-sand; in dried condition: light gray, strongly coherent. 12.18 % Ca CO<sub>3</sub>.

The bottom-sample contained 0.36 % carbon.

Station 48. 61° 32' N. L., 15° 11' W. L., depth 1150 fm., bottom-temp. 3.17°. Bøggild; Globigerina clay, in moist condition: light gray, coarse sand-clay; in dried condition: whitish gray, loosely coherent. 54.72 % Ca CO<sub>3</sub>.

The bottom-sample contained 0.32 % carbon.

Then follow 4 stations, lying north of the above-mentioned Ridge. The bottom-temperature is negative. The stations 101, 110 and 112 lie almost in a straight line, running in a north-easterly direction from the north-east coast of Iceland. Station 116 lies close in to Jan Mayen.

Station 101. 66° 23' N. L., 12° 05' W. L., depth 537 fm., bottom-temp. ÷0.7°. Bøggild: gray, deep-water clay, in moist condition: bark bluish gray, very fine clay; in dry condition: bluish gray, very coherent. 0.48 % Ca CO<sub>3</sub>.

The bottom-sample contained 1.64 % carbon and 0.162 % nitrogen; quotient  $\frac{C}{N} = 10.1$ .

Station 110. 66° 44' N. L., 11° 33' W. L., depth 781 fm. Bottom-temp.



÷ 0.8°. Bøggild: Transition clay, in moist condition: brownish clay-sand, in dry condition: light brownish, fairly coherent. 8.75 %  $\text{CaCO}_3$ .

The bottom-sample contained 0.83 % carbon.

Station 112, 67° 57' N. L., 6° 44' W. L., depth 1267 fm. Bottom-temp. ÷ 1.1°. Bøggild: Globigerina clay, in moist condition: light-brown, sandy clay, in dry condition: very light-brown, very coherent. 46.32 %  $\text{CaCO}_3$ .

The bottom-sample contained 0.42 % carbon and 0.0414 % nitrogen. Quotient  $\frac{C}{N} = 10.2$ .

Station 116. 70° 05' N. L., 8° 26' W. L., depth 371 fm. Bottom-temp. ÷ 0.4°. Bøggild: Transition clay, in moist condition: dark brown-gray, sandy clay, in dry condition: light brown gray, fairly coherent. 9.60 %  $\text{CaCO}_3$ .

The bottom-sample contained 0.718 % carbon.

Lastly, one station situated between Iceland and Greenland was investigated and is remarkable for its extraordinarily high percentage of lime.

Station 90. 64° 45' N. L., 29° 06' W. L., depth 568 fm. Bottom-temp. 4.4°. Bøggild: Globigerina clay, in moist condition: light gray-brown, clay-sand, in dry condition: brownish white, fairly coherent. 57.00 %  $\text{CaCO}_3$ .

The bottom-sample contained 0.48 % carbon.

**6. Conditions for the deposition of organic matter on the bottom of the sea.** The object with the carbon analyses mentioned above is twofold. On the one hand, the numbers are to be used to throw light on the organic material contained in the bottom-soil. This factor, as will be shown later, plays an important role in the animal life on the sea-bottom. Further, the data are also to be used to throw light on the conditions, under which the organic matter is deposited on the sea-bottom, and especially where it originates from.

The first question we shall endeavour to answer is, therefore, under what conditions the organic matter is deposited. The materials deposited by the sea are sorted out before deposition, so that the heaviest materials are precipitated in waters most in motion, and the lightest at the still places. The organic materials belong to the last group all the more the more finely divided they are. The specific gravity approximates very much to that of the water. We may say therefore, briefly, that the organic materials with regard to their deposition follow the clay particles.

This is distinctly seen also from several of the above analyses. The bottom consists of almost pure sand, so far as is known, over large stretches of the shallow North Sea, where the water is almost always in motion. The clay particles are only present in very small quantity and the same is the case with the organic matter, as analysis shows. Only 0.35 % carbon was found. In the Kattegat, as Chart III in the atlas of the »Hauchs Togter« shows, the bottom is somewhat different. Down to a depth of 15—20 meters the bottom consists of sand, from a depth of ca. 20 down to a depth of ca. 30 meters we meet with the so-called mixed bottom with varying quantities of sand and clay, and it is only outside a depth of 30—35 meters that we find pure clay deposits, the so-called blue clay. Determinations of the quantity of organic matter on sand bottom and the mixed bottom are not available. But several analyses have been made of

the clay bottom, which all show, that the quantity of organic matter out there is fairly large, namely, about 2 % carbon.

Passing from the Kattegat into the fjords, there is much less movement in the water, and corresponding to this the clay particles and the organic material are deposited in much shallower depths. Here we must go into a depth of 2—3 meters to find the sandy bottom. Already at a depth of 5 meters we meet with the strongly clayey soil, which composes the greater part of the bottom in our fjords and Bredninger, and from which the majority of the above-mentioned analyses originate. As will have been seen, we have at least the same amount of carbon as in the Kattegat at 35 meters depth.

**7. Origin of the organic matter on the sea-bottom.** When we pass now to consider more closely, where the organic material of the sea-bottom comes from, whether it is the vegetation of the *Zostera* belt or the plankton organisms which play the greatest role in this regard, we must first make sure, what the carbon analyses given above indicate and for what purpose they can be used. As shown, we have determined the percentage quantity of carbon in the uppermost part of the bottom-soil in dry condition, and the numbers indicate therefore only the quantity of carbon or organic matter in relation to the inorganic material which exists in the bottom-soil.

Owing to the relative value of these figures, we must therefore, to obtain results from them, proceed with very great caution. That one place of the sea-bottom shows more organic material than another, does not necessarily mean, that at the first place more organic matter is deposited annually. Possibly this is simply due to the fact, that relatively little inorganic matter is deposited at the first place, but a relatively large quantity at the other place. With this in mind we way now consider the analyses from the Limfjord.

We may begin with a comparison of Louns Bredning with Livø Bredning. Louns Bredning belongs to the inner reaches of the Limfjord. Through Virksund it is connected with Hjarbæk Fjord and through Hvalpsund it opens out into Livø Bredning. Both Louns Bredning and Hjarbæk Fjord are very shallow. According to the Chart (see Beretn. f. Biol. Stat. VI, 1895, pg. 32) only a little over  $\frac{1}{3}$ rd of Louns Bredning lies outside the 6 meter line, and in Hjarbæk Fjord a depth of 6 meters only occurs at all in the channel which leads in through Virksund. We may therefore expect an extremely rich *Zostera* vegetation. On the Chart prepared by Ostenfeld to show the distribution of the *Zostera* in the Limfjord (cf. Ber. f. Biol. St. XVI, 1808, pg. 27), these Bredninger are unfortunately not included; but both from information received from Petersen as from personal observation I know that there is an extremely rich *Zostera* vegetation at these places. Hjarbæk Fjord in fact is even almost quite covered with *Zostera*.

Livø Bredning on the other hand is considerably deeper and the shores are steeper. About  $\frac{2}{3}$ rds of Livø Bredning lies outside the 6 meter line, according to the above Charts. Nor does the *Zostera* vegetation cover so much ground in Livø Bredning, as a glance at Ostenfeld's Chart will show. The largest growths are found in Draaby Vig on the east coast of Mors.

With regard to the proportion of plankton in Louns and Livø Bredning, we have only a single estimate in the VIIth Report of the Biological Station for

1897. It appears from this that the »density« of plankton in Livø Bredning was 7.5 against 1.7 in Hvalpsund (Louns Bredning). A single determination like this is naturally very little to build upon, when it is a question of the quantity of plankton throughout the year; but there is nothing which indicates or suggests, that in the inner reaches there is more plankton than in Livø Bredning for example; we should much rather expect the reverse.

We may now consider the condition as regards the quantity of organic material in the sea-bottom at the two places. In the bottom-sample from Louns Bredning there was 4.3 % carbon, and in the bottom-sample from Livø Bredning (west of Furhoved) there was only 2.21 % carbon, thus the first place had almost double that of the second.

The question is now, whether there is reason to believe, that in Livø Bredning more inorganic material is deposited annually than in Louns Bredning. The answer is, that there is rather reason to believe the opposite; Louns Bredning is much more shut in by the land, so that there is both the possibility of erosion from the coasts and the best conditions for the deposition of the eroded materials.

If we cannot assume, however, that in Livø Bredning twice as much inorganic material is deposited annually as in Louns Bredning, then the determinations given of carbon can only mean, that in Louns Bredning more organic matter is annually deposited than in Livø Bredning. Thus, there seems to be some proportion present between the richness of the *Zostera* vegetation and the quantity of deposited organic matter, but not between the latter and the density of plankton. We believe, therefore, that we may conclude from this, that the main source of the organic matter in the sea-bottom must be due to the *Zostera* belt and not to the plankton organisms. In choosing Louns and Livø Bredninger to illustrate this matter, I may say that it was entirely arbitrarily. We could have obtained the same result from many other localities. This may be shown in a little more detail.

Beginning with the North Sea, we find there but little organic material out in the sea-bottom. This is probably due to the fact, that not much organic matter is produced in the North Sea, and that there is not enough calm for the deposition of organic material. Passing from this into Nissum Bredning, the quantity of organic matter rises at once from 0.34 to 0.56, and gradually as we penetrate further into the Limfjord, to Kaas and Thisted Bredninger where the *Zostera* vegetation becomes more extensive, the quantity of carbon in the bottom-soil also becomes greater, namely from 1—2 %. It never reaches so high as in the innermost reaches, Louns Bredning for example, with the richest *Zostera* vegetation, or in the deep channel off Glyngøre, into which the rich *Zostera* vegetation of Nykøbingbugt is carried out and deposited.

We come to quite the same result on considering the conditions in Isefjord, where the proportion between the quantity of *Zostera* and the quantity of organic matter deposited on the sea-bottom is if possible even more distinct than in the Limfjord. The bottom in Roskilde Bredning, where we find large quantities

of *Zostera*, is covered as mentioned above with a meter-thick layer of black, stinking mud with an amount of carbon of no less than 10.2 %. The same is the case, though to somewhat less extent, with Bramsnæsvig and Holbæk Fjord. Information regarding the quantity of *Zostera* in the last-mentioned is given by the Chart in the I. Report of the Danish Biol. Station. On the other hand, as soon as we come out into the broad reaches of Isefjord, where the *Zostera* decreases, the quantity of carbon in the bottom-soil also decreases. It declines to 2.27 %.

In the Kattegat, as shown above, the *Zostera* is of far less importance than in our fjords, and we might perhaps be surprised that the two bottom-samples from the Kattegat, the one from Anholt, the other W. N. W. from Kullen, both contained over 2 % of carbon. This is explained by the fact, that the portion of the Kattegat, which is sufficiently deep to permit of a deposition of organic matter, constitutes a fairly small part of the whole area of the Kattegat. A large part of the Kattegat is fairly clean sand, a still larger part a mixture of clay and sand. Of these the sand bottom only contains quite inappreciable quantities of organic matter (according to the analyses from the North Sea; we have no analyses from the sand bottom in the Kattegat). It is only when we come out to a depth of over 30 meters that we find the deposits of blue clay, and it was from this soil that the analysed bottom-samples were taken. As Chart III in the atlas of »Hauchs Togter« shows, this kind of soil is of very small extent, so that the material produced in the Kattegat is concentrated on a relatively small area; on the other hand, the percentage of carbon must be fairly high. Further, there is perhaps a by no means inconsiderable transport of *Zostera* from the Belt Sea. In any case large masses of seaweed are often met with floating in the Belts and the Kattegat.

We may now pass from the home waters to a consideration of the bottom analyses from the Ingolf Expedition. Common to all the bottom-samples examined, with exception of that from Station 101, is that they contain extremely little carbon in comparison with the bottom-samples from the Danish waters. This agrees perfectly with the above-quoted statement of Murray and it harmonizes well with the idea, that the source of the organic material in the sea is mainly the plant-formations bound to the coasts, the algae and *Zostera*.

We may notice further, that it is the bottom-samples which come from nearest the coast which contain most carbon. This is shown by the bottom samples from Stations 45—48, which lie in a line running towards the west from the Færoes.

Station 45, which lies nearest the land, contains the largest quantity of carbon. It is even more distinct, however, in the determinations from the stations north of Iceland. The station nearest Iceland, 101, contains fairly considerable quantities of carbon namely 1.64 %, whilst Station 112, which lies furthest away from land, only shows 0.42 %. This difference becomes even more obvious when we consider, that the largest quantity of inorganic material is undoubtedly deposited in under the land. Since, nevertheless, the percentage of carbon is much greater there, this can only mean that in under the land more organic matter is annually deposited than out in deep water, in other

words, the organic matter in the sea-bottom is mainly derived from the benthos formations at the coasts.

In describing the bottom-soil in Thisted Bredning I remarked that a large part of the organic particles in the soil are intensely coloured by Ruthenium-red, but not by chlor-zinc-iodine. This indicates that the organic material in the bottom-soil consists of pectose and not of cellulose. It appears also, that the cell walls of the *Zostera* leaves likewise contain very little cellulose, but on the other hand much pectose. This also indicates that the organic matter in the sea bottom is mainly derived from the *Zostera* belt. A further chemical investigation of this condition will perhaps give interesting results.

The result of these investigations is, therefore, that it is the plants of the *Zostera* belt and not the plankton organisms which constitute the principal source of the organic matter in the sea-bottom. Since now this organic material, as will be shown later, is the main nourishment for the benthos fauna, Lamellibranchs, worms etc., and these again for several of our food-fishes, it follows, that it »is certainly this plant, which for a great part conditions the fish-wealth of our coasts and attracts the fishes from the open and deeper waters into the shallow, enclosed bays and fjords« (C. G. Joh. Petersen, I. Ber. f. D. biol. Stat., 1890) — a conception which finds confirmation in these investigations.

8. **Bacteria life in the bottom-deposits.** Bottom-deposits which contain organic matter are naturally the dwelling-place for a rich bacteria life. The strong smell of sulphuretted hydrogen given off especially by the more muddy bottom-samples at once reveals this. We singled out Roskilde Bredning above as the place where the largest quantity of organic matter was found. The bottom consists of a quite black, strongly odorous mud several meters thick. If we push a pole down into the mud we see the air-bubbles rising up to the surface, coming obviously from the gases collected down in the mud. Some of this gas was collected in a sodawater bottle over water and analysed more closely. Hydrogen sulphide does not seem to be present. A quantity of the gas was driven over into a Hempel pipette filled with glass balls and copper sulphate and stood for 24 hours without any part of the gas disappearing. Further, the gas contained very small quantities of oxygen and carbonic dioxide. Some of the gas was analysed for inflammable gases, particularly methane; it was mixed in an explosion-tube with oxygen and the mixture ignited. The ignition followed the equation:



The quantity of carbonic dioxide formed is thus, measured in volumes, equal to that of the methane in the gas. After the ignition, the gas remaining was analysed for carbonic acid and found to contain ca. 80 %. The gas thus contains ca. 80% methane. It should be remarked, that the gas before analysis was cleared of carbonic dioxide.

Certain fermentative processes are thus going on in the mud of Roskilde Fjord which lead to the formation of methane. As shown by Omeliansky

methane is formed by the fermentation of cellulose; but it is quite possible, that methane may be formed by the fermentation of other substances, e. g. pectoses.

But besides this formation of methane there is a formation of ferrous sulphide in the mud on the bottom of Roskilde Fjord. The black colour of this mud is mainly due to ferrous sulphide. Adding acid to the mud, it assumes a somewhat lighter colour. The same happens, when the mud remains in the air, the ferrous sulphide being oxidized. In an undried bottom-sample from Roskilde Fjord the quantity of ferrous sulphide was determined in the following manner. The bottom-sample was boiled with addition of water on the water-bath to drive off the free hydrogen sulphide. Then an excess of sulphuric acid was added to free the hydrogen sulphide, which was driven out by heating up the water-bath and carrying through a stream of air. The sulphuretted hydrogen was absorbed in ammoniated silver nitrate. The silver sulphide precipitated was filtered off, dissolved in nitric acid and precipitated with hydrochloric acid. From the silver chloride precipitated, the combined sulphuretted hydrogen was calculated to amount to 0.38 % of the dried material. The method is not altogether exact, and the result is probably somewhat too low; but it shows that the quantities of ferrous sulphide formed are fairly considerable.

A detailed study of the formation of ferrous sulphide in freshwater has been made by Beyerinck: »Ueber Spirillum desulfuricans als Ursache von Sulfatreduktion« (Centrbl. f. Bact. 2 Bbth., 1, 1895 p. 1, 49 and 104). He remarks first of all, that the sulphide formation by organisms may proceed in the following 4 ways: (1) by splitting up the sulphur-containing albuminous materials; (2) from sulphur (3) from sulphites and thiosulphates, where the last must be split up first of all into sulphur and sulphide; (4) through reduction of sulphates. It is the last mode of formation which is most important in nature; in the canals of several Dutch towns this formation of sulphide of iron is extremely troublesome. The bacteria which causes the reduction of sulphates is anaerob. In order that this may be able to develop, the water must first be deprived of its oxygen. This desoxidation of the water is due to other bacteria, the growth and development of which are conditioned by the presence of organic materials in the water. Simultaneous with the production of the ferrous sulphide in the water, the quantity of the sulphates is reduced.

The formation of sulphide of iron in saltwater seems to proceed under the same conditions as in freshwater, though it is probably other bacteria which effect the reduction. The parallel which, according to the above, must exist between the quantity of organic matter and the sulphate reduction, can also be readily shown in our fjords. The blackest and most stinking mud, which certainly also contains the greatest quantity of ferrous sulphide, is found in Roskilde Bredning, where we also have the greatest quantity of organic matter; but it is certain, that Holbæk Fjord and Bramsnæs vig also contain large quantities of ferrous sulphide. In the Limfjord again, it is the places where most organic matter is found, that we meet with the ferrous sulphide, in Louns Bredning for example; on the other hand, not in Thisted, Kaas and Livø Bredninger. In Vilsund we have a sandy bottom with remains of *Zostera* buried in the sand. It was of interest to note, that the *Zostera* remains and the sand lying around these were

coloured black by the ferrous sulphide, whilst the greater part of the sand was free of ferrous sulphide, thus evidence of the parallelism mentioned between organic matter and formation of ferrous sulphide. The clay bottom in the Kattegat (samples from Anholt) does not contain sulphide of iron; but if we allow such a sample to stand in the glass-tubes above-described for taking up the samples, we see after some time that round, black patches of sulphide of iron begin to form a little distance under the surface. It is clear, therefore, that a reduced supply of oxygen here leads to the production of ferrous sulphide.

The occurrence of ferrous sulphide in the sand on our coasts of the North Sea has been shown by Warming (Kgl. Vid. S. Skr. 7 R II, 1904).

We find in the literature various notices regarding the fact, that arms of the sea (fjords in Norway) and whole inland seas (Black Sea) can become uninhabitable to animals owing to the lack of oxygen. This has usually been explained by saying, that the animals use up the oxygen in the water, when it is not sufficiently renewed by inlets and outlets. These explanations certainly only contain a part of the truth. It is scarcely the animals which have brought the Black Sea into the condition in the deep water, which is described by Zernòv (*Inter. Revue d. ges. Hydrobiol. og Hydrogeogr.* II., pp. 99—123, 1909, III p. 226, 1910). The hydrogen sulphide region of this Sea is rather due to the extremely rich plant production, which is great enough, along with the slow renewal of the water-masses, to form a bottom-soil containing a large amount of organic matter. In this way the possibility is created for a rich bacteria life, production of hydrogen sulphide and so on, which certainly contribute to a very high degree to deprive the water of oxygen. The Black Sea is briefly an example of the conditions which have been described above for our inner fjords, only in a much more advanced stage. Curiously enough, so far as known to me, similar conditions are not met with everywhere in freshwater where plant materials are deposited in great quantities: here the preserving action of the humic acid probably has some influence (peat-bogs). We may therefore, to a certain extent, regard the large oceans as the lungs of the sea, which supply the water-masses of the inner seas with oxygen and remove the superfluous organic matter.

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#### IV. Organic matter in the sea-water.

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In the introduction to the chapter on the deposition of organic matter on the sea-bottom, we mentioned how the plants of the *Zostera* belt were carried away from their original grounds and at last in more or less finely divided condition deposited on the sea-bottom. It is the water of the sea which achieves the transport. It is of interest now to follow the organic matter on the way from the place of production to the place of deposition, namely in the sea-water itself;

since even in this stage the organic material plays a great part in the economy of the sea.

1. **Historical summary.** It was Johannes Müller, who first remarked that a quantity of small organisms, plants and animals, occurred floating in the sea; he fished them up by means of gauze nets and called them »Auftrieb«. Hensen (1882 p. 1) introduced the expression plankton; with this he understands: »alles was im Wasser treibt, ob hoch oder tief, ob todt oder lebendig.« Through Hensen numerous investigations of the plankton have been carried out. The method in these investigations is, as known, that the plankton is fished with the plankton net of silk gauze with different, but always very small width of mesh. The plankton fished in these nets consists almost exclusively of organisms, plants and animals mixed. Of dead material, which according to the definition should also belong to the plankton, there is very little. Planktology is thus practically the study of the microscopic animals and plants which float in the water.

As time went on, however, the view was gained, that the plankton which could be fished in the plankton nets, the »net plankton«, as it is now called, only represented a part of the plankton found in the water. Kofoid filtered the water through hardened filters and thus found, that the ordinary plankton nets of millers' gauze only caught 2,2—50 % of the total plankton. Almost about the same time Lohmann (1902, p. 1) found in the gut of *Appendiculariae* numerous small organisms of which nothing was seen in the net plankton. Now the *Appendiculariae* are themselves a kind of plankton net. By means of a sieve apparatus, which is simply many times finer than the plankton nets, they are able to filter the sea-water which passes through them. Thus, organisms must occur in the sea-water which cannot be detected in the net plankton because they are too small and pass through the nets.

It was necessary, therefore, to seek for other methods which could help in the study of the plankton. Such a method was found in the centrifugal apparatus (cf. especially Lohmann, 1908). The specific gravity of the plankton is greater than that of the water, and the plankton can thus be almost completely precipitated by means of such a centrifugal apparatus. In this way Lohmann showed, that in addition to the plankton organisms occurring in the nets, there is a large number of small organisms, which are so small that they pass through the nets; and he found, further (l. c., p. 347), that large quantities of dust-fine detritus occurred as well as the plankton organisms.

Recently Pütter (»Die Ernährung der Wassertiere«, 1909) has emphasized the presence of dissolved organic matter in seawater. Pütter relies here on analyses from the Mediterranean made by Natterer (Polaexpedition 1ste u. 2te Reihe 1893—1894). By means of the permanganate method, to be mentioned later, Natterer determined how much oxygen was required for the oxidation of the organic material in 1 litre of seawater. He found that from 1.90—2.85 mgm. were required, in one case even 6 mgm. of oxygen (the figures from Pütter). Further, Raben (Wiss. Meeresunters. N. F. Bd. 11) has investigated the quantity of organic material in the Kiel Fjord and Baltic by means of a modification of Messinger's method. He found that 3.0—13.9 mgm. of organic combined carbon occurred in 1 litre of water. The water was filtered before analysis.



With regard to the nature of the dissolved, organic matter, Pütter refers to some analyses of Natterer, who isolated from 200 litres of seawater a substance whose melting point indicated that it was palmitic or stearic acid. Further, on vapourizing the remaining substance in a vacuum a product was distilled which was diagnosed as glycerine. It seems possible also that humus compounds must be present, as they play a great part in many freshwaters.

As result of the above, we may conclude that 3 groups of organic substances occur in saltwater, namely, plankton organisms, detritus and dissolved organic material.

2. **Methods.** The apparatus and methods used in the study of the organic materials occurring in seawater are the following:

1. Centrifugal apparatus (Gärtner's); in this there is room for 7 tubes of the ordinary kind, conical at the one end. Each tube could contain ca. 15 ccm. water, so that 105 ccm. of water could be centrifuged at one time. The apparatus was worked by means of a leather belt and was kept in movement for 10 minutes (cf. Lohmann). After this a fine siphon was used to draw off all the water with exception of  $\frac{1}{2}$ —1 ccm.; the precipitates in the tubes were stirred up in the water remaining and the contents of all the tubes thrown together into one tube, which was centrifuged again. In this way a single tube came to contain the plankton and detritus of ca. 100 ccm. water.

Lohmann has made a thorough critical investigation of the usefulness of the method, and reference may be made to his work.

2. Detritus-collectors. All the organic and inorganic material floating in the sea, whether detritus or living organisms, will in the end, if not dissolved beforehand, sink to the bottom, the organisms however only after death. Thus there is a constant process going on of material falling to the bottom of the sea. To take up this material and thence to determine the quantity which in any unit of time falls to the bottom, Petersen has worked out an apparatus which we call a »detritus-collector«. It consists of an iron cylinder, closed below with a wooden bottom. Its diameter is 30 cm., its height the same. To prevent the iron rusting, which would cause the precipitated plankton to be mixed with rust, the iron cylinder is covered on the surface with a layer of cement. The quantity precipitated in such a detritus-collector is an expression for the quantity of plankton + detritus which in the time chosen sinks down through a plane in the water with an extent of  $\frac{1}{15}$  m<sup>2</sup> and lying 30 cm. above the bottom. As the water in such a collector, owing to its small diameter, is always at rest, the material which is once deposited will remain where it is.

3. Oxidation by means of potassium permanganate. To determine the quantity of both the dissolved and deposited organic matter (detritus-plankton organisms) I have used oxidation with potassium permanganate in the form indicated by Schulze. In the case of seawater the determinations must always be made on alkaline solutions, as the chlorine set free by the sulphuric acid in acid solutions has a reducing action on the potassium permanganate.

Water-samples of 500 ccm. taken with the water-bottle were used for the analyses. The water-samples were preserved by the addition of 10 ccm. sublimate solution and kept in bottles with glass stoppers. For the analysis 2 samples, each

of 100 ccm. water, were used, the one being centrifuged, the other not. The amount of organic matter found in the centrifuged sample gives the quantity of dissolved organic matter in 100 ccm. water. The difference between the quantity of organic matter found in the uncentrifuged and the centrifuged sample gives the quantity of suspended organic material (plankton + detritus).

The analyses were carried out in the following manner. To 100 ccm. of water 20 ccm. of a ca.  $\frac{n}{100}$  potassium permanganate solution were added (in 1 liter water ca. 0.33 gm. potassium permanganate is dissolved) plus  $\frac{1}{2}$  ccm. of a sodium hydrate solution (1 part of caustic soda in 2 parts water). The mixture was boiled for 10 minutes, then cooled to 50—60°, and 5 ccm. of dilute sulphuric acid were added (1 part concentrated sulphuric acid to 3 parts water). Further 20 ccm.  $\frac{n}{100}$  oxalic acid were added. This will give an excess of oxalic acid in the liquid, and the amount of this excess is determined by titration with potassium permanganate solution. So much of the latter solution is added until a permanent, very faintly rose tone appears. We have now determined, how many ccm. of potassium permanganate solution are required to oxidize the organic materials in the water + 20 ccm.  $\frac{n}{100}$  oxalic acid solution. We now add, whilst the liquid is still maintained at the same temperature of 50—60°, a further 20 ccm.  $\frac{n}{100}$  oxalic acid solution and determine by titration, how many ccm. of potassium permanganate solution are required to oxidize 20 ccm.  $\frac{n}{100}$  oxalic acid solution alone. The difference between the quantities of potassium permanganate solution used gives how many ccm. of this solution are required to oxidize the organic matter in the analysed sample, and at the same time we obtain the strength of the potassium permanganate solution accurately determined in relation to the  $\frac{n}{100}$  oxalic acid solution. 1 ccm.  $\frac{n}{100}$  potassium permanganate solution means 0.08 mgr. oxygen.

An example will illustrate this. For the first titration (oxidation of 20 ccm. oxalic acid + the organic materials in 100 ccm. water) 26 ccm. of potassium permanganate solution were used. For the second titration (oxidation of 20 ccm. of the oxalic acid solution) 19 ccm. of the potassium permanganate solution were used. The difference between the two titrations, 7 ccm., thus gives the number of ccm. of potassium permanganate solution, which is used to oxidize the organic matter in 100 ccm. At the same time we know (through the second titration) that the potassium permanganate solution is of such a strength, that 9.5 ccm. of potassium permanganate solution are used for 10 ccm.  $\frac{n}{100}$  oxalic acid solution. Thus 7 ccm. corresponds to  $\frac{7 \times 10}{9.5} = 7.4$  ccm.  $\frac{n}{100}$  oxalic acid solution; in other words, to oxidize the organic material in 100 ccm. water we required in the case chosen 7.4 ccm.  $\frac{n}{100}$  potassium permanganate solution.

### 3. Quantitative determinations of dissolved and suspended organic matter.

I may now briefly discuss the results obtained by means of the above methods; beginning with the determinations made by the potassium permanganate method (cf. the accompanying tables).

The following remarks may be added to these tables. The number of analyses is, as will be seen, fairly small and the water-samples chosen somewhat accidental. In this direction the investigations have not been carried out suffi-

## 1. Limfjord.

	Water not centrifuged	Water centrifuged	Dissolved organic matter	Suspended organic matter
1. North Sea, W. of Agger, 16 m. depth, $\frac{7}{7}$ 10 . . . . .	4.1	3.8	3.5	0.3
2. Nissum Bredning, close to Fjordgrunden, $3\frac{1}{2}$ m. depth, depth of bottom $4\frac{1}{2}$ m., $\frac{7}{7}$ 10 . . . . .	4.5	3.7	3.7	0.8
3. Kaas Bredning, middle, $5\frac{1}{2}$ m. depth, depth of bottom $6\frac{1}{2}$ m., $\frac{7}{7}$ 10 . . . . .	7.4	6.9	6.9	0.5
4. Thisted Bredning, off Sennels, 7 m. depth, $\frac{9}{8}$ 10 . . . . .	5.0	4.8	4.8	0.2
5. Thisted Bredning, Surface, $\frac{21}{5}$ 10	4.8	4.6	4.6	0.2
6. Louns Bredning, 5 m. depth, depth of bottom 6 m., $\frac{6}{7}$ 10 . . . . .	5.2	5.2	5.2	0.0
7. Hjarbæk Fjord, 3 m. depth, $\frac{25}{5}$ 10 . . . . .	8.3	5.9	5.9	2.4
8. Off Egholm, Surface, $\frac{18}{5}$ 10 . . . . .	9.1	9.2	9.2	0.2
9. Off Ulvegabet, Surface, $\frac{18}{5}$ 10	6.8	›	›	›

## 2. Isefjord and Kattegat.

	Water not centrifuged	Water centrifuged	Dissolved organic matter	Suspended organic matter
10. Roskilde Fjord, Store Bredning, surface . . . . .	10.0	10.0	10.0	0.0
11. Nedre Draaby Bredning, surface, $\frac{10}{5}$ 10 . . . . .	7.5	5.7	5.7	1.8
12. Kattegat, off Isefjord, surface, $\frac{10}{5}$ 10 . . . . .	7.4	5.1	5.1	2.3
13. Kattegat at Anholt, 25 m. depth, $\frac{11}{5}$ 10 . . . . .	5.0	›	›	›

ciently systematically, and the determinations given can only be regarded as quite provisional. I have not wished to omit them, because no others have been made for our waters and because I believe that, in spite of their imperfection they may yet be used as an illustration; but they must naturally be used with the greatest caution.

The figures in the table give the number of ccm. of an  $\frac{n}{100}$  potassium permanganate solution required to oxidize the organic materials, dissolved or suspended, in 100 ccm. water. With some exercise the determinations can be made with an accuracy of  $\pm 0.2$ — $0.3$  ccm. of potassium permanganate solution.

The water-samples were taken with a water-bottle. The number behind the locality indicates the depth at which the sample was taken. In a few cases the depth of the bottom is also given.

The first thing that strikes one on considering the analyses given is, all the samples contain dissolved organic matter in not so very small quantities. It is also of interest to compare these results with the determinations made in other waters; for example, Natterer's determinations from the Sea of Marmara (1895). Natterer has determined, just as I have done, how many ccm. of an  $\frac{n}{100}$  potassium permanganate solution are required to oxidize the organic materials in 100 ccm. water. He found that from 2.8—14 ccm. potassium permanganate solution were used. Taking the average of his determinations we find that it amounts to 7.93 ccm.; the average of my determinations for the Limfjord and Isefjord (not centrifuged water) is 6.57, thus a figure of almost the same size.

A comparison with Raben's determinations, which were made after Mes-singer's method, is not possible, as we cannot calculate the quantity of the oxidized organic matter from the amount of oxygen used. The amount of oxygen, namely, differs for the different kinds of organic materials, and the oxidation is in many cases incomplete. So far as one can see, however, the results found by means of this method are also of about the same size as those found by means of the potassium permanganate method.

Returning now to my own investigations, if we go from the North Sea into the Limfjord we find an increase in the quantity of the organic material dissolved in the water, from 3.8 in the North Sea to 6.9, 4.8 and 4.6 in Thisted and Kaas Bredning. It will be noticed that we have here a complete parallel with the bottom-analyses discussed in the preceding section. We saw, that the quantity of the organic matter in the sea-bottom also increased, when we pass from the North Sea into Thisted and Kaas Bredning. In the inner reaches of the Limfjord, in Louns Bredning and Hjarbæk Fjord, the quantity of the organic matter dissolved in the sea-water rises to respectively 5.2 and 5.9, and in the eastern part of the Limfjord (off Eegholm) to 9.2.

There is almost always a steady current of water through the Limfjord from the North Sea to the Kattegat. The analyses show, that this current as it passes through the Limfjord becomes richer and richer in dissolved organic matter, a condition which is also evident by merely observing the colour of the water in the Limfjord. In the western part of the Limfjord the colour of the water is gray-green, when the weather is calm, in the eastern part of Livø Bredning (about at Løgstør) the appearance changes and assumes the brownish colour, which is

characteristic for the eastern part of the Limfjord and for the inner reaches (e. g. Louns Bredning). This brownish Limfjord water can be followed a good distance out into the Kattegat off the mouth of the Limfjord.

Pütter (1909 pp. 108 and 127) has put forward the view, that the dissolved matter in sea-water comes from the plankton algae, which he regards as »sugar manufactories«. Without entering upon a criticism of Pütter's evidence, which seems to me not specially convincing, I may remark that my data rather indicate, that the dissolved organic matter, like the organic matter in the sea-bottom, mainly comes from the benthos formations, at any rate in our fjords. In the Limfjord there is more dissolved organic matter in Hjarbæk Fjord than in Thisted Bredning, and in Roskilde Bredning there is almost double as much dissolved organic matter as in the mouth of Isefjord. This agrees fully with the occurrence of the organic matter in the sea-bottom, and we may therefore conclude, for the reasons shown in the preceding section, that the dissolved organic matter also mainly comes from the benthos formations.

The quantity of the organic matter suspended in the sea-water is, as can be seen from the tables, of very variable proportions. On the whole it is fairly small; in two cases, in Louns Bredning and Thisted Bredning, no suspended organic matter at all could be found in the sea-water by the permanganate method, most was found in Hjarbæk Fjord and in Isefjord, where half as much suspended as dissolved organic matter was found.

It seems as if the winds play a very great part in the occurrence of suspended organic matter in the sea. In the beginning of July, when a series of water-samples was taken (Nos. 1, 2, 3, 6), the weather was calm, and we see that extremely little suspended organic matter occurs in these water-samples. Sample 10 was also taken in calm weather. On the other hand, samples 11 and 12 were taken after a heavy storm; in both we find a fairly considerable amount of suspended organic matter. I shall return later to this point; first of all we may enquire as to the nature of the suspended matter.

**4. Microscopic examination of the material suspended in the water.** In the foregoing we have investigated the quantity of the suspended matter; we may now investigate, of what it consists. A microscopic examination of material centrifuged from the sea-water gives the following results. The larger part consists of detritus, a mixture of dust-fine, organic and inorganic materials in such a finely divided condition, that we can no longer determine what it originally came from. Here and there we find pieces a little larger, which can be seen to consist of the tissues of higher plants, as also shells of diatoms, *Peridineae*, bristles of Annelids, bits of *Copepoda*, rarely a whole copepod, starch grains, strands of cotton, in fact, with sufficiently careful search we can find everything which might possibly end in the sea in sufficiently finely divided condition.

But what is of special interest and what I wish to emphasize especially, is the inappreciable part played by the plankton organisms in relation to the quantity of detritus. In July, when the water in the Limfjord, as the plankton nets showed, contained large quantities of *Chatoceros*, a series of centrifuging experiments was made; only in quite a few cases did we find a single *Chatoceros* among the centrifuged material. That the reason for this was not that

the *Chaetoceros* organisms could not be centrifuged, was proved by centrifuging a quantity of *Chaetoceros* taken in the plankton nets and placed in the water. The water could not be centrifuged quite clean, it is true, but the main quantity of the *Chaetoceros* was nevertheless collected at the bottom of the centrifuging tubes.

The so-called »nannoplankton«, which passes through the plankton nets and which according to Lohmann's investigations plays a considerable role in the western Baltic, seems not to have any great importance in the Limfjord according to the investigations made up to the present. I have seen extremely little of these organisms in the centrifugal experiments I have made.

5. **Origin and quantity of the matter in suspension in the sea at the different times of the year.** I mentioned above a 3rd apparatus for the study of the quantity of plankton and detritus, namely, the detritus-collectors. I may now briefly discuss the results obtained by means of this apparatus.

The detritus-collectors give us, as already explained, an expression for the quantity of suspended matter, which within a certain period of time sinks down through a plane in the water  $\frac{1}{15}$  m.<sup>2</sup>, situated 30 cm. above the bottom. In the course of the year the detritus-collectors have been put out at various places, most frequently in Thisted Bredning, once in Nissum Bredning. One difficulty with the use of the detritus-collectors is that they are often destroyed by the fishermen. We had 3 collectors in the beginning, but of these one was lost in the course of the summer.

The detritus-collectors are taken up at intervals of a half or whole month. The greater part of the water is poured off, and the remainder carefully emptied out by means of a glass. When but little water remains, the deposit is stirred up and the whole transferred into high glass-tubes, where the deposit is again allowed to settle. Then the last portion of the water could be removed, and the deposit preserved by the addition of alcohol. On arrival in Copenhagen, the alcohol was evaporated, the deposit dried in quite the same manner as the bottom-samples and then weighed. In a few cases a determination of the carbon in the deposit was made.

In addition to the weight of the material found in the detritus-collector within a certain time, the following table shows how much will be deposited in the same time per  $\frac{1}{10}$  m.<sup>2</sup>, as also how much is deposited daily in the given period per  $\frac{1}{10}$  m.<sup>2</sup>

1. Thisted Bredning, 12 meters depth, 1.—15. April 1910.  
1 detritus-collector contained 1.81 gm.  
per  $\frac{1}{10}$  m.<sup>2</sup> 2.72 gm., per day 0.19 gm.
2. Thisted Bredning, 12 meters depth, 15.—22. April 1910.  
In 1 detritus-collector 2.35 gm.  
per  $\frac{1}{10}$  m.<sup>2</sup> 3.54 gm., per day 0.51 gm.
3. Thisted Bredning, 14 meters depth, 25. April—21. May 1910.  
In 1 detritus-collector 39.8 gm.  
per  $\frac{1}{10}$  m.<sup>2</sup> 59.2 gm., per day 2.24 gm.
4. Thisted Bredning, 7 meters depth, 4. June—5. July 1910.  
In 1 detritus-collector 1.47 gm.  
per  $\frac{1}{10}$  m.<sup>2</sup> 2.22 gm., per day 0.07 gm.

5. Thisted Bredning, 10.5 meters depth, 6. July—10. August 1910.

In 1 detritus-collector 29.8 gm.

per  $\frac{1}{10}$  m. 44.7 gm., per day 1.28 gm.

6. Nissum Bredning, 26. September—29. October.

In 1 detritus-collector 117 gm.

per  $\frac{1}{10}$  m. 175.5 gm., per day 5.16 gm.

A microscopic examination of the material deposited in the detritus-collectors shows the same picture as has already twice been described, namely, under the description of the brown surface layer on the bottom in Thisted Bredning and under the description of the suspended matter centrifuged from the sea-water.

The principal mass of the organic material deposited in the detritus-collectors consists, as in the two other cases, of detritus — a mixture of fine inorganic particles, only a small part of which can be diagnosed.

A chemical investigation of the matter deposited in the detritus-collectors gave the following result. Detritus from Thisted Bredning contained 2.8% carbon. It will be remembered that the uppermost, brown layer on the bottom of Thisted Bredning contained 3.06% carbon, thus almost the same result. Detritus from Nissum Bredning contained 1.79% carbon. The bottom-analysis from Nissum Bredning given in the preceding section contained only 0.56% carbon; but this analyses did not refer, as in Thisted Bredning, to the uppermost layer alone. In that case it would certainly have given a somewhat higher value. It seems clear, therefore, both from the microscopic and the chemical investigation, that the material obtained in the detritus-collectors is completely identical with the uppermost brown layer on the sea-bottom.

If we consider the data given above, which show the quantity of material deposited in the detritus-collectors per day, we see at once, that the numbers vary very greatly. In the period from 4. June—5. July 0.07 gm. is deposited per  $\frac{1}{10}$  m.<sup>2</sup> and day, whilst from 25. April—21. May 2.21 gm. are deposited daily, thus over 30 times as much. This confirms what we have already discussed under the determination of the organic matter suspended in the sea-water, that the wind plays a great part in the suspension and thus also in the precipitation of organic and inorganic matter in the sea. As will be remembered, June of 1910, in which so little material was deposited in the detritus-collectors, was on the whole remarkable for fine and calm weather.

The origin of the matter deposited in the detritus-collector is certainly twofold; on the one hand, there is a constant transport, especially when the water is in motion, of inorganic and organic materials from the shore and the plant belt out into the sea, where they are deposited; on the other hand, the detritus, which has already been deposited on the bottom, is stirred up anew, certainly during strong winds, and then again deposited. This may obviously be repeated several times. The large quantity of detritus, which is deposited in the detritus-collectors,

shows that it is the detritus on the sea-bottom, which in any case at times is the principal source of the detritus deposited in the detritus-collectors.

## V. Food of the animal life, especially in Danish fjords.

It is many years since I first dissected oysters in the Limfjord in order to study the contents of their digestive organs; I imagined that they must live on the plankton which is so rich at times, but I was always extremely surprised to find their gut filled with an indeterminable, fine-grained, grayish or brownish mass, in which could be seen relatively few diatoms (mostly bottom-forms), a few *Peridineæ*, annelid bristles, spores, bristles of *Crustacea* etc. The most common organism after the bacteria is clearly *Prorocentrum micans*, but only a slight importance can be ascribed to it, so far as mass is concerned.

I have investigated these conditions at different times of the year from March to November; in the true winter months there seems on the whole but very little in the gut of the oyster.

The indeterminable mass cannot be distinguished in any essentials from the dust-fine detritus, »ooze«, which is found on the bottom where the oyster lives. We now know, indeed, that detritus forms the uppermost brown layer on the bottom of the whole of the Limfjord outside the plant belt. No recognizable difference has ever been seen between the organisms in these detritus layers and in the contents of the gut of the oyster, but the larger objects in the layer at the bottom naturally do not occur in the oyster. The quantity of organisms in the gut and stomach of the oyster is so small, that I must consider it as certain, that its food mainly consists of the organic parts of the detritus. It is possible, however, that the oyster at other places, where the quantity of detritus is less than in the Limfjord, may find its food, for example, mainly in diatoms or other small organisms. In Holland Redeke in 1902 showed similar conditions regarding the food of the oyster, especially that the material in its stomach had almost nothing to do with the plankton forms at the spot. Redeke describes a similar condition in *Mytilus edulis* and *Ascidella aspersa*. He comes to the conclusion, however, that the diatoms are the main food, and not the »donkergrijze drabbige Massa«. Whether it is the one or the other which in reality is the main thing, will certainly depend on which contains the most accessible food; both presumably are of importance in this connection. So long as we do not have direct investigations on what the oyster really can digest in its stomach, I am of the opinion that we must have regard for both the detritus and the living organisms in this. Lotsy (Rep. U. S. F. C. for 1893, pp. 375—386) refuses all importance to the detritus as food, because it apparently passes through the digestive tract unchanged; but it seems to me that there is absolutely no justification for this view, an exact examination is wanted. In the American oyster Lotsy found, in addition to diatoms, at least just as large a mass of »decaying



organic matter«; thus a great deal of detritus was also found here. He mentions, that he could fish the same diatoms in quantity with the pelagic net in the surface waters; but as he does not give the names of these, it is impossible to determine whether he has really found pelagic diatoms in the stomach of the oyster or not. In shallow water there does not always seem to be sharp boundaries between the pelagic diatoms and those living at the bottom.

Lotsy's view of the small importance of detritus for the oyster, seems to have also influenced other American investigators. H. F. Moore (R. U. S. F. C. 1897, rep. 1903) thus writes p. 318: »The food of the oyster consists entirely of minute animal and vegetable organisms and small particles of organized matter«; but in 1907 »Survey of oyster bottoms in Matagorda Bay, Texas« (Bureau of Fisheries document No. 610, 1—86 pp.) he only mentions the diatoms and small organisms found in the stomachs of oysters, and not at all the »small particles of organized matter«. He figures the commonest of these on 3 Plates; most of them belong to the genera *Coscinodiscus*, *Melosira*, *Synedra*, *Navicula*, *Pleurosigma*, and also *Prorocentrum micans*. Nearly related or identical forms are found in the oyster of the Limfjord; true plankton forms thus also seem rare in the stomachs of the American oyster. Moore however has made some very careful, quantitative determinations of the quantity of these organisms, both in the water and in the oyster and writes on p. 80, that the most surprising thing was, the small amount of food consisting of such organisms he found in the oyster: — — »the average stomach content of all oysters examined to be about one-eighth cubic millimeter, less than one-tenth the volume of the head of an ordinary pin«. It would be difficult to wish for a better proof, it seems to me, that it is not these small organisms which constitute the chief food of the oyster. Nor does Moore seem entirely satisfied with the result of his investigation. He has later continued his work on this subject, in order to determine the quantity of diatoms in the stomach contents of the oyster (Bull. Bureau Fish. Vol. XXVIII 1908 [1910]); but he has not yet come to any definitive result.

I may also just mention, that the study of the dissolved organic matter in the sea-water had previously been considered in connection with the food of the oyster, before Pütter in recent years brought it forward again. Lotsy loc. cit. investigated the water in which the oysters lived for dissolved organic material, but he states that scarcely a trace of this was found in the many chemical analyses made; he therefore attaches no importance to this matter.

The experts of the Dutch Government seem to have laid a great deal of weight on the evidence brought forward by Redeke, that it is the bottom-forms, and thus the ground, which is of the greatest importance for the nourishment and growth of the oyster; and it was certainly of importance to show, that what is usually called »plankton« was not the principal food of the oyster; but soon new inexplicable factors appeared. Thus, the oysters can live on large stones or rocks far above the bottom, i. e. they are not bound to the diatoms of the bottom or its detritus. Both in Scandinavia and Italy (Fusaro) the oyster is found to feed hanging in the water on iron boxes and the like; Otto Pettersson in Sweden and Helland-Hansen in Norway (Intern. Rev., Bd. I, pp. 353—73,

1908) have described how the oyster thrives well on an iron threadwork net, stretched high above the bottom.

E. Rauschenplat in his, in so many respects, excellent work »Ueber die Nahrung von Thieren aus der Kieler Bucht« (Wiss. Meeresunt. Kiel. Neue Folge. 5. Bd. 1901) has described how the animals, which he calls plankton-feeders, never contain pure plankton, but at the same time large quantities of detritus. His explanation of this is, that ships' screws, fish nets, perhaps waves and currents stir up the bottom of the deep water in Kiel Bay, so that the detritus becomes mixed with plankton out on the muddy bottom; the animals attached to piles or other objects above the bottom also contain detritus, and the reason for this, according to Rauschenplat, is that the waves break against these and tear away small parts of plants, of pieces of wood and suspended sand grains or masses of detritus collected among the heaps of Lamellibranchs, so that the water thus becomes unclean. He ascribes great value to the detritus as food; but that it should actually be present everywhere in the water-masses themselves, seems never to have occurred to him. I had also believed in this »pile-theory« for a long time, which indeed I had constructed for myself. It was Boyesen Jensen's centrifuging experiments in 1909 on »pure« Limfjord water, which first showed me, that there is at least often and probably always more detritus than plankton present in the water itself. In 1908 appeared Lohmann's excellent work »Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton« (Wiss. Meeresunt. Kiel, N. E., Bd. 10. 1908), in which on the basis of centrifuging sea-water he shows, that the whole plankton content of the water cannot be determined by means of the older methods, certainly not by nets of fine millers' gauze; far too many small organisms pass through; various species are not caught at all. He endeavours further to show, that even if all the plankton is included, there is in winter not enough plant food to supply the requirements of the plankton animals: »so muss man nach einer weiteren Nahrungsquelle für die Planktontiere suchen und die ist, wie mir dünkt, in dem überall im Meere verbreiteten Detritus in grosser Menge gegeben«. Here for the first time I find the idea, that the detritus present in the water-masses themselves is an essential source of food for the plankton animals. He seems to have grave doubts as to whether the large diatoms of the net-plankton have any appreciable importance as source of food, and he believes that the view, that the *Copepoda* feed on them, has not been proved (see however Dakin's later investigations 1908). But to return to the food of the Limfjord oyster. Here we have a mass of water full of dust-fine detritus, »wet dust«, of the same nature as the contents of the stomach and gut of the oyster and the uppermost brown layer on the bottom of the fjord. Whether now the oyster obtains its detritus from the detritus lying on the bottom which has been stirred up in one way or another, or whether it obtains it from the detritus sinking down through the water itself, is of less importance. Oysters kept in a box a couple of meters above the bottom contain essentially the same after 8 days as oysters lying under them on the bottom; a certain sorting out of the material can be detected however, but no qualitative difference. It has thus taken long, before one could believe the evidence of one's eyes, that the oyster is a detritus-feeder, and that in addition it

probably makes use of the animals and plants it may find among the detritus in smaller or larger number. The many annelid and copepod bristles and other hard, small parts of animals and plants, as also the siliceous parts of plankton diatoms, found in the detritus of the stomachs, have undoubtedly contributed to spread the belief, that many animals feed on the plankton; most of these remains must rather be regarded however as parts of the detritus itself, as it is obviously only after the organisms have died and sunk to the bottom, that they have been eaten along with the rest of the detritus.

The impression gained of the nature of the bottom from dredging has certainly also contributed to the belief, that the detritus of the bottom was useless as food; the often black, stinking layers of mud, which lies under the uppermost brown layer, is what strikes the eye most; and they are probably indeed of no use as food for higher organisms. On being stirred up into the water, however, they very soon change their character and colour, a fact I have been able to observe, for example in aquaria. That one cannot detect the difference between the dust-fine detritus in the stomach and gut of the animals, also gives the impression that it is not digested (Lotsy); Rauschenplat rightly replies to this, however, that such a difference cannot be seen either in the animals which are known to live on detritus, as certain Gephyreans and other worms, loc. cit. p. 93. Rauschenplat cites Möbius, who in 1871 already had written, that the Lamellibranchs in the Baltic feed on »Moderteilchen der toten Pflanzen«; this was before attention had been directed to the importance of the plankton. Möbius' view was thus unbiassed and certainly in many cases more correct. See also Möbius: 1ste Ber. Wiss. Untersuchungen. Kiel. 1873 p. 139.

It is certain that no other detritus-feeding animal has been so carefully studied as the oyster; we know much less about the other detritus-feeding animals in our fjords, therefore, but that there are many of them, is undoubted.\*) In Rauschenplat's paper we find good information regarding stomach contents of the animals occurring in Kiel Bay. He refers certain worms, among others *Arenicola* and *Pectinaria belgica*, as also *Diastylis Rahtkii* among the *Crustacea*, to the true detritus-feeders, further though with doubt *Ophioglypha albida*. To the plankton-feeders he refers *Aurelia*, *Balanus*, *Mysis*, Ascidians and a number of the commonest Lamellibranchs; but he adds: »reines Plankton habe ich nur ganz vereinzelt in den verdauenden Kavitäten gefunden« and he emphasizes this statement in print; he also states expressly that he often just in the plankton-feeders finds an »unkenntliche Masse« in the digestive tract: »Ob es sich um Verdauungspro-

\*) I do not wish to leave this question of the food of the oyster without referring to the »green oysters«, which are found in France and various other countries, and whose green colour in several parts of the body, especially the gills, has been placed in connection with the occurrence of certain green plants, in France *Navicula fusiforme* var. *ostrearia*, on which they are supposed to feed. Referring simply to one work on this subject, the literature on which is very great, namely Herdman and Boyce: Oysters and disease (Lancashire Sea-Fisheries Memoir, Nr. 1, 1899), I may mention, that it seems as if oysters are coloured green in several ways and not always by the same substance; and that it is not settled, that the green colour comes from organisms which have passed through the digestive canal of the oyster. It does not seem to have been rightly investigated what the oyster really has in its stomach; the green colour especially cannot with certainty be said to come from digested diatoms.

dukte oder um Detritus in der feinsten Form handelt, habe ich mit Hilfe des Mikroskopes nicht entscheiden können«. Since we now know, that with us in the Limfjord and most probably in all waters with dense vegetation, the »plankton« is mainly detritus, the matter is placed in another light; but to make any difference between detritus-feeders and plankton-feeders thus becomes in fact impossible. For this we should require to find certain species, which were able to filter the detritus from the plankton, in order to feed on the latter alone; but according to Rauschenplat's tables such are very rare, in *Cynthia rustica* alone has he sometimes found »sehr reines Plankton«, and in *Cynthia grossularia* sometimes »reines Peridine-plankton«; but often there was also much impure plankton and »unkenntliche Masse«. It would be better perhaps to distinguish between animals, which take their food from the water by filtration and animals which directly feed on parts of the uppermost brown layer of the bottom; the result will often be very much the same, however, only the method is different. Certain worms, Lamellibranchs and Echinoderms certainly take their food from the bottom itself, but most of the other detritus-feeders, as many Lamellibranchs, Holothurians etc. from the water.

Rauschenplat mentions lastly a group of animals which live on »flesh-food«, namely various, probably all, fishes, larger Crustacea, as crabs and shrimps, most of the *Nereidae* and *Asterias rubens*, and animals which live on fresh plants. Under these are placed *Idothea*, many *Gammaridae*, also *Littorina littorea* and *Acera bullata*; a special division, which lives on small plants, especially bottom-diatoms, is formed by *Rissoa octona* and *Cerithium reticulatum*.

In 1909 appeared a work by E. Eichelbaum: Über Nahrung und Ernährungsorgane von Echinodermen. Kiel, 4<sup>o</sup>, pp. 1—88 (Wissens. Meeresunt. Bd. XI. Abt. Kiel), in which the food of the Echinoderms was studied on animals collected partly at Kiel partly in the North Sea. Reading through the orderly tables on the food contents of the digestive organs we are at once struck by the very large quantity of »Bodenmaterial« present in them; he refers none of the Echinoderms investigated by him to the plankton-feeders. Regarding *Echinocardium cordatum*, for example, whose stomach content is always bottom-material, he writes: »Der Darm ist mit Bodenmaterial stets prall angefüllt und die Bewohner dieses Meeresbodens bilden die Nahrung des Seeigels«; something similar is said regarding the nearly related forms. That the bottom-material could of itself be of great importance as food, he does not seem to have grasped; on p. 71 however he says in a summary on »Irrigulares«: »Meeresboden und die in ihm lebende Tiere«.

I would also refer here to a work by E. Ehrenbaum: »Zur Naturgeschichte von *Crangon vulgaris* Fabr.« (Sonderbeilage 3. d. Mitt. d. Sekt. f. Küsten- und Hochseefischerei. 1890). He has closely studied the food of the shrimp both in the open and in stomachs; he finds that the larvae contain »eine breiige Detritus ähnliche Masse« — »in der gerformte Theile nicht mehr zu erkennen waren«; later however he mentions diatom skeletons in this and that among other things plant remains must play a certain role for the larvae. I believe that the larvae must also be regarded as detritus feeders. The adult *Crangon* on the other hand often feed on pure mud (»Schlick« he calls it) from the bottom, their stomachs are full of it and they have a peculiar taste at that time; at other times they feed on worms, *Amphi-*

*poda* and *Schizopoda* and then become of a better taste and also change in their outer appearance. This animal is thus as adult sometimes detritus-feeder, sometimes predatory. In this Ehrenbaum is undoubtedly right; his careful investigations might have made both Rauschenplat and Eichelbaum careful in drawing conclusions from stomach investigations on a material collected incidentally for other purposes. Their subdivision of animals into predatory, detritus-feeders etc., must therefore also be treated with care; — the boundaries are very often deleted in nature.

In the »Report for 1899 on the Lancashire Sea-Fisheries Laboratory, 1900« J. Johnstone describes, p. 36, what *Cardium edule* contains in its stomach, namely, in addition to sand and fine ooze, which is the principal mass, spores, stages of lower algae, Foraminifera, diatoms and small microscopic Crustacea; which of these is their principal food, he does not mention. In an earlier Report he has stated, that nothing is found as a rule in the digestive tract of *Cardium*, it is quite empty. I mention this, because I have found a similar condition in *Buccinum* (see below). A very extensive literature might be cited on the stomach contents of marine animals; but I do not think we should get any further in the matter in this way, and I shall therefore go over to a discussion of my own investigations on this subject.

To obtain accurate knowledge regarding the food of the animals, I have preferred to investigate a restricted animal community, and have taken as special basis for these investigations one of the most restricted divisions of the Limfjord, Thisted Bredning. As the tables in the next section will show, an insight has been gained with regard to the mass per m.<sup>2</sup> of each single species, so that we are able, at least for the part lying outside the plant belt, the soft clay bottom, to determine both by number of individuals and by mass, which species are predominant. Table V, autumn 1910, shows, that *Mya truncata* is in mass quite the dominant form with 240 gm. dry matter per 10 m.<sup>2</sup> against 282 gm. dry matter per 10 m.<sup>2</sup> for all species. The remaining Lamellibranchs contributed ca. 21 gm. Of other animals *Ophioglypha* is abundant in numbers, in 1910 with 457 individuals per 10 m.<sup>2</sup>, but with only 2.74 gm. dry matter, calcareous matter not included; further *Pectinaria* with 3.70 gm., other worms with 5.72 gm. Of the gastropods only *Buccinum* and *Nassa*, with together 5.83 gm., are worth mentioning.

The content of the Lamellibranchs' stomachs is the finest detritus with the relatively few, living, small organisms occurring therein, which only to a small extent have anything to do with plankton organisms.

In 1911 I fitted up a small aquarium with detritus as bottom and then had the opportunity of watching how *Abra alba* obtained the detritus. With the one, longer siphon it literally sucks in the uppermost layer of the bottom; the detritus can be seen passing through the transparent siphon; after taking several helpings, it throws out a part of the stuff, only the very finest passes through the animal. It is thus a bottom detritus-feeder. Meyer und Möbius (Fauna der Kieler-Bucht 1865—72) also mention that they have seen *Abra* in the aquarium taking in bottom-particles through the one siphon. Other Lamellibranchs, which do not have long siphons, must presumably take their detritus from the water directly; but these questions require to be more closely investigated in aquaria. It

is interesting to see, how Lamellibranchs such as *Abra* are able to a certain extent to sort out the detritus entering through their siphon; this will certainly hold good for all Lamellibranchs.

In the animal community the Gastropods and *Asterias* must be regarded as predatory animals; but though it may be very easy to capture the whelks on pieces of cod, (*Buccinum* and *Nassa*), it is just as difficult on the other hand to ascertain what they eat under normal conditions; their stomachs are almost always empty or contain a slime, the origin of which it has not been possible to determine.

In the above-mentioned aquarium I have had the opportunity to see, how *Fusus antiquus* was able to open *Mytilus edulis* of almost the same length as the whelk and then eat up the soft parts. The whole method of the opening of the Lamellibranch however requires to be further investigated; I am inclined to believe, that a secretion from the whelk has in some way a paralysing influence on the mussel. If this whelk can open Lamellibranchs, then it is certain that *Buccinum* and *Nassa* can also do so.

That *Asterias rubens* feeds on Lamellibranchs, I consider as beyond all doubt; on the one hand I have found, for example, *Abra* in its stomach and on the other I have seen it devouring *Mytilus edulis* both in nature and in the aquarium. *Ophioglypha* often takes only fine food, I have seen detritus with bottom-diatoms in its stomach. The occasional occurrence of shells of small molluscs in its stomach may perhaps be regarded as due to chance. The species occurring in Thisted Bredning is *O. texturata*, but the individuals are fairly small. The investigations of both Eichelbaum and Rauschenplat agree with mine in the fact, that *Ophioglypha* contains much bottom-material in its stomach. R. seems to regard it as in half part a plankton feeder, but I do not quite understand his statement (p. 149), and E. regards it as a predatory animal, which specially seeks after *Polychaeta*; he has found the remains of worms among the contents of its stomach. I have sometimes found comparatively pure quantities of bottom-diatoms in its stomach; one would almost think that it knew how to select them in one or other way. In the aquarium I have seen it standing up in the soft mud on all 5 arms, so that the disc was raised just above the bottom; in this way perhaps the cavity formed with its 5 small exits may help in one way or another to collect the bottom-diatoms just under the mouth. In the aquarium I have seen *O. albida* throw itself with great rapidity on cut pieces of the soft parts of Molluscs, which shows that the Ophiurids are not always content with detritus-food; but I have never seen them attack living *Abra* in the aquarium. I am inclined with Eichelbaum to consider them as worm-feeders: but the whole matter must be more closely investigated.

On the detritus-bottom in Thisted-Bredning we thus have a **detritus-eating, Lamellibranch-worm community with its predatory animals**. This animal community forms the basis for a great part of the fish-life there, but this subject will be dealt with in a later section.

When we come closer in towards the land, into depths of ca. 5 meters and less, we meet with the *Zostera* belt as a rule and its fauna; for

practical reasons\*) quantitative investigations have not yet been carried out here, but it may be said with certainty that this is the region of the small gastropods, *Rissoa*, *Trochus*, *Cerithium*, *Littorina*, *Lacuna* and Nudibranchs; here we also find *Modiolaria* (*marmorata*, *discors*) and *Mytilus*, mostly young, as also a quantity of Amphipods, Isopods, and all the animals which swarm on the *Zostera*, as Hydroids, *Actiniae*, *Echinus miliaris*, Ascidians (*Ciona*, *Clavellina*), worms etc. Inside the *Zostera*, on more or less pure sand bottom, often with stones, we meet lastly the strand-fauna with *Fucus* and other algae as the characteristic plants. In the pure sand in here live *Mya arenaria*, *Cardium edule*, *Tellina tenuis*, *Arenicola marina* and on stones and plants especially *Acmæa*, *Chiton*, *Littorina littorea*, *Balanus* etc.; in this innermost belt quantitative investigations are also difficult, among other reasons because the »Sallingsund« cannot go in on such shallow depths and the apparatus is too heavy to be used from an ordinary boat. In the Sound this belt is further out in deeper water, 8—9 feet, and some quantitative determinations were carried out here, Table VI, Snekkersten. The fauna of the pure sand bottom resembles the fauna on the clay bottom with regard to the life; it consists of Molluscs and worms, which are detritus-feeders; but the remaining, plant-covered part of the strand-belt and the fauna of the *Zostera* belt is, as has been shown in the above sketch, more mixed. Here live Lamellibranchs (*Modiolaria*) and Ascidians as detritus-feeders, which obtain their detritus from the water itself, along with Gastropods which either feed upon the *Zostera* itself or its algal vegetation, or they lick off the slime on the surfaces of the older leaves of the *Zostera*, on the stones or other objects, oysters and the like. *Acmæa* and *Chiton* actually keep the upturned shells of oysters free of plants, but in doing so dig deep passages in the shells. *Littorina littorea* is used at certain places to keep the oyster basins free of the algae which grows on them.

From my experiments with bundles of twigs, stones, shells and such like objects, laid out for the oyster spat to attach themselves to, I know how quickly such objects in the Limfjord become covered with a slimy layer consisting of quite small plants, among which certainly bacteria and lower algae play the most important part; to get the spat-catchers out just at the right moment is the main thing, as the layer of slime prevents the small oysters from attaching themselves. The *Gobies* also seek for clean objects to fasten their eggs on and in the spawning-time almost every object which is laid out on the bottom, such as anchors, stones, cigar boxes and the like, are covered over with the eggs in the course of 24 hours. This shows, how much clean objects are sought after, in other words, how much the algal slime occurs in these plant belts, where the influence of the light is still felt strongly right to the bottom. The blades of *Zostera*, with exception of the very young, are all covered over with this slime, and every one knows the large colonies of algae and diatoms which grow on the *Zostera* and

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\*) In the Tables I—III (cf. Chart I) some of the stations 91—100 at any rate should perhaps rather be referred to the *Zostera* belt, on almost all of them some *Zostera* grows as a matter of fact. The animals taken there are also essentially different from those of the other stations; there does not seem to be very many of them. Regarding the animal life of the *Zostera* region in general, I cannot venture to express an opinion, so far as the quantity is concerned, until further investigations have been carried out.

transform each single leaf to a »lamp-cleaner«. I consider these small, slime-forming algae a very essential component of the food of the animals which live in these regions, and Rauchenplat's investigations, which show among other things that the stomachs of Gastropods are filled with bottom-diatoms and pieces of algae in addition to pieces of *Zostera*, indicate just that this is the case.

In 1899 K. Brandt wrote with reason: »Diese schnell sich vermehrenden kleinsten Pflanzen der Uferregion werden augenscheinlich starker gefressen, als die grossen Tangbüsche und die kieseligen Seegräser.«

Among all the dead oysters with the shells still connected I have fished up in this shallow water, I have only found two containing soft parts; all the others had been cleaned by the flesh-eaters such as *Asterias* and Gastropods, and this occurs very quickly, as direct experiments with cast-out, opened oysters have shown me. The two dead oysters with the soft parts were quite rotten and stinking, and were both found at the same time early in the spring, shortly after the ice had disappeared, thus presumably before there was much life in the lower animals of the shallow water. Otherwise an opened oyster is deprived of all its soft parts in 24 hours, at any rate in summer; an index of how quickly and cleanly everything is eaten up which has any value as food. In these two plant belts live almost all the animals which Rauchenplat calls large-plant feeders and small-plant feeders, as also predatory animals and flesh-eaters. Among the inhabitants of the plant belt I have sought in vain for animals, which contained plankton forms in their stomachs to any essential degree. The beautiful *Clavellina lepadiformis* which is always attached to objects above the bottom and might be expected to feed on such organisms, is always filled with detritus, in which however a quantity of Lamellibranch larvae, Tintinnids and other plankton may be found.

There remains for consideration only the food of the true plankton animals and the fishes. Among the latter there are but few, which as adults can be referred to the plankton-feeders, probably only the herring and sprat, which occur in quantities in the Limfjord at certain times of the year; there the herring also feed on bottom-forms, such as worms; I have not made systematic investigations in this region in this connection\*).

With regard to the actual consumers of the plankton, there is still great

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\*) In his paper (Chemische Zus. d. Planktons, 1900. pp. 45—46) Brandt states, that herring and mackerel feed almost entirely on plankton organisms, that *Cyclopterus* in the aquaria feeds on *Aurelia*; but even the other fishes, which eat larger animals, therewith take the plankton into themselves for the most part in altered form. The herring certainly eat, and perhaps mostly, Copepods but also many other forms with us; the stomach contents of *Cyclopterus* may also be said to be remains of Medusae; but most of the other economically important fishes certainly do not eat plankton, not even in altered form; it does not hold good in any case for the fishes of our waters. I have seen *Acanthias vulgaris* in the Great Belt often filled with *Pleurobrachia* alone, at times they eat the same in the North Sea, but at other times as known they take more solid food. I only mention this as an example of, how varied the food of fishes is, and to utter a warning against drawing wide reaching conclusions, without numerous investigations in nature, with regard to what the different fishes mainly live on in reality in the different waters. That the larger animals, on which so many fishes feed, should be regarded as »Plankton in altered form«, is such a general expression, that it is difficult to prove; it certainly does not hold good for the most of our waters: where and to what an extent it may prove to be correct is a work for future investigators.



uncertainty as to the food of these animals in spite of the older and more recent investigations, for example Dakin's. I shall not endeavour to discuss this matter in detail here, but merely refer to the Kiel investigations (Hensen, Brandt, Lohmann), which show that the mass of the plankton animals, at least at several places and at different times, is much greater than the mass of the plankton plants, so that it is difficult to understand, where the animals get their food from; even if we include the commonest organisms (*Vollplankton*), Lohmann is still of the opinion, that at certain times at least, in the winter, we must look round for other sources of food than the plants and he refers to the dust-fine detritus. We should not believe, therefore, that the plankton at such times has anything left over for the food of the bottom animals, or that it has for them any importance on the whole, except perhaps as detritus-formation, especially in the form of dead animals and excrement.

In his famous work of 1887 Hensen endeavours, naturally quite provisionally and as a sort of estimate, to give an idea of the annual production of plankton per m.<sup>2</sup> in the Western Baltic, where the water is ca. 20 meters deep, and he came to the result, that of the really organic dry-matter, not silicate, ca. 150 gm. are produced annually, but ca. 134 gm. of this was based on a few experiments with the feeding of Copepods in closed bottles; for the other animals there should thus remain only ca. 16 gm. per m.<sup>2</sup>, presumably not only for the bottom-animals but also for the plankton animals. The whole production of 150 gm. per m.<sup>2</sup> is not small in comparison with the production of hay on the land, it is almost the same; but the amount remaining for the benthos fauna is obviously too little. The amount of dry matter in these is often 28—35 gm. per m.<sup>2</sup> in the Limfjord, and in this fjord with its shallow water the quantity of the plankton according to my investigations is not in any way so great as in the Kattegat or in the Belts. Further, the existing bottom-fauna must as a matter of fact eat its own weight several times in the course of a year if it is to live and grow, so that far too little material is obviously left over from the plankton for its nourishment. We cannot attach any very great accuracy to the results of these preliminary reports, nor does Hensen do so; I have only mentioned them in order to show, that their results are not in opposition to what has been displayed above, namely, the importance of the detritus and plankton in the Limfjord.

Whilst very fine detritus is clearly of advantage for the growth of many animal species, I must nevertheless agree with Lohmann (1909 p, 227) when he says, that the great quantities of detritus in the coastal waters is »lästig« for several plankton organisms. He has touched upon an important problem here — the absence of certain plankton organisms from the neighbourhood of the coasts, in spite of high salinity and suitable temperature etc. Is it not likely to be the dust-fine detritus, which is directly harmful to many clean-water organisms? I have often seen quantities of the pelagic forms of the North Sea, such as e. g. *Pleurobrachia*, floating in with the current into the Limfjord, but rapidly perish and go to the bottom covered with a thick gray layer of the detritus which is so plentiful in the western parts; on the other hand, other plankton organisms are able to bear this detritus.

In this connection I may mention, that Brandt has shown in the Kiel Canal, that there is there but a very sparse plankton in spite of a rich bottom

fauna. He is of the opinion, that this condition can be explained in this way, that new plankton often, almost daily in fact, is carried by the current into the Canal, and that what is present is eaten up by the bottom-animals; I think, that the condition can be explained in a much more natural manner from the large deposits of detritus. (See Brandt: *Wiss. Meeres. IV. Bd. Kiel. 1899*, p. 226, Note and Mitt. *Deutsch. Seefischerei v. 1897*, pg. 232—241).

At many places in the salt-water it is naturally more difficult to obtain information regarding the importance of the plankton in quantitative regards for the food of the fauna, than in freshwater, as the latter is sometimes quite enclosed; but the results obtained hitherto do not seem to indicate that the plankton plays any great role in the food question of the fishes. Wesenberg-Lund writes in »Ymer« 1909, (Part I, pp. 132—133) as follows: »With regard to fishery questions it has hardly been made clear, that the plankton does not play nearly so important a part for the useful fishes of the freshwater as for those of the sea. Not a single one of the former lives as adult on plankton. — Even if we might say that the young live partially on plankton, this description of the food of the young is on the whole erroneous. Its food should much rather be called the lower animal and plant world of the littoral zone —.«

In the recently published Nr. 1 of the »Deutsche Fischerei-Zeitung« 1911 B. Schiemenz states (p. 2): »dass der Auftrieb (Plankton) nur für wenige Fische als Hauptnahrung in Betracht kommt, dass aber die meisten unserer Süßwasserfische und auch unsere sämtlichen Teichfische sich von der Ufer- und Bodenfauna ernähren und der Auftrieb (Plankton) nur als Gelegenheits- oder Notnahrung in Betracht kommt — —«. He shows further, how the word plankton in regard to freshwater has been misused and gradually come to include everything that occurs on occasion in the water, even the organisms which really belong to the bottom; we should return to Hensen's definition of the plankton, he says. As contrast he uses the word »Aufwuchs«, by which he understands: »diejenigen Organismen, die auf den Pflanzen und andere Gegenständen des Ufers and flachen Wassers wachsen und sich herumtreiben.« »Dieser Aufwuchs ist es nun, der sehr wesentlich als Fischnahrung in Betracht kommt.«

These are the opinions of men who have studied the biology of our freshwaters for many years; for a long time many seem to have overestimated the importance of the plankton as a source of food, and I am inclined to believe, that at least the same has been done in the case of our coastal seas.

I shall not seek to penetrate deeply on this occasion into what is known regarding the metabolism of the freshwater, as I have not made investigations in this field: but a study of recent literature, E. Walter, Schiemenz, Zuntz, Knauthe, Knorrich etc., seems to me to indicate definitely, that even if disagreement exists as to what should be called plankton and what not — a disagreement which has perhaps tended to accentuate the differences of opinion — yet all are agreed, that the dissolved and suspended, organic materials in the water as well as the detritus on the bottom coming from dead bottom-plants, are of great importance as food for the animals. (Schiemenz: *Anhang pp. 200—201 in Max. von dem Borne: Künstliche Fischzucht, 5te Ausgabe 1905*, and E. Walter: *Die Karpfennutzung in kleinen Teichen, 1909*,

pp. 16—17). Walter certainly endeavours, so far as I understand him, to insert an intermediate link between detritus and the Crustacea, namely »die aller kleinste, mikroskopische Algenflora«; but he only does this partially; older investigations (Knørrieh) show, that the Daphnidae can live and propagate in sterilised solutions, where such algae do not occur. (Knauthe's book 1901, pp. 152—153). Thus, a complete understanding of the dust-fine detritus does not seem to have been reached for the freshwater either, but the matter has been much further advanced than for the salt water; here investigations have been too one-sided.

It often happens indeed, that a line of study becomes more one-sided than its discoverer originally, in this case V. Hensen, intended. On reading his first, great work on plankton of 1887 we see, that he had indeed considered the possibility that the sources for the food-stuffs of the sea are also the rivers and the coasts (p. 1); but he does not ascribe any considerable importance to this source, because: »ich finde nämlich thatsächlich nur eine sehr geringe Menge treibenden Materials, welches von den Küsten her stammt«, and further: »weil, soweit mir bekannt geworden, überhaupt nur sehr wenig Thiere von abgestorbenem Materiale leben.«

We may remember, that it has only been in recent years, that the quantity of dust-fine detritus in the sea-water has been demonstrated by centrifuging, it is only from this that its importance for animal life can be properly understood and estimated.

On the page cited Hensen defines the plankton as »Alles was im Wasser treibt, einerlei ob hoch oder tief, ob tot oder lebendig.« Judging from the words this definition also embraces the dust-fine detritus; but this was not known at that time; if we reckon all floating detritus to plankton, then this comes for the most part just from the coasts at certain places, that is the animal and plant life of the bottom, and is thus something quite different, in its origin at any rate, from the benthos.

If we also reckon the dust-fine detritus, coming from *inter alia* the benthos plants, to the plankton, then we must expressly admit this and remember, that this detritus is found both in the water and on the bottom, as also that it may be present where no other plankton is found; it was certainly present for example in Hensen's aquarium, and may be produced by the organisms by the bottom alone. Nor in the future should the word plankton be used without defining exactly what is intended therewith (net-plankton, nannoplankton or detritus-plankton), or without remembering that benthos and plankton in any case at many places are closely connected. The breeder of carp who does not take into sufficient consideration the role the vegetation of the bottom plays, will certainly come to regret it.

Though Hensen thus believed, that dead organic material served the animals for food only to a small degree, and that the vegetation of the coasts is of small importance as source of food compared with that of the plankton, he is one of the few who has really made experiments to study the matter closely. He writes for example loc. cit. p. 101, that »Die Erzeugung des Meeres an der Küste muss eine sehr bedeutende sein«; by digging in the sand at low tide he found incredible masses of lower animals on small areas: »es muss hier eine sehr grosse

Menge von Nahrung zur Verfügung stehen.« He has constructed an aquarium just to study this matter more closely and writes on the results of these experiments at the same place. The principal production in this aquarium provided with bottom plants, in which plankton could not be got to live, was Amphipods, which fed on the plants, *Fucus vesiculosus* and *Florideae*. The quantity of the *Amphipoda* became so great, »dass meine Erwartungen in Bezug auf das sich entwickelnde Leben in manchen Richtungen übertroffen worden sind.«

Hensen has thus shown, that marine animals in a aquarium can live without »plankton«, and even propagate and increase in quantity considerably in the course of 2 years. Unfortunately such experiments have certainly rarely or never been made since. This shows, that Hensen has known, that the vegetation of the coasts may also be of importance, though he only ascribes it a small role in the food of the sea; that many of his successors in the study of the plankton have so little remembered this, is therefore not due to Hensen.

In a work published in 1893 by Friedr. Dahl of Kiel, one of Hensen's colleagues (Untersuchungen über die Thierwelt der Unterelbe. Wissens. Meeresunters. Kiel VI Bericht. 1893), which deals with the bottom-fauna in the mouth of the Elbe and contains among other things quantitative determinations of the number of animals per m.<sup>2</sup>, investigated by digging at ebbtide, we find on p. 180: »Hensen begann die Untersuchung mit dem Plankton, weil dieses für die genannten Bestimmungen am besten zugänglich schien — —«. »Die Methode ganz allgemein auf die am und im Grunde lebenden Organismen auszudehnen, ist bisher noch nicht gelungen.« Dahl refers here to quantitative determinations of the organisms living together at one place, and he makes these by digging at low-water.

In the »Deep-Sea Deposits« 1891 of the Challenger Expedition, p. 252, John Murray already protested against making the quantities of plankton in the sea the sole basis for judging the organic contents of the latter; since large quantities are carried out to sea from the land, rivers and from coastal regions.

C. Apstein in »Das Süßwasserplankton, Kiel 1896« discusses very carefully pp. 102—106 the different sources of the food-stuffs in a freshwater; he also recognizes other sources than the plankton.

K. Brandt (Wiss. Meeresunt. Kiel 1899, Bd. 4, p. 222) mentions, that several authors, as Frenzel and Schiemenz, the one for freshwater the other for coastal waters, consider the importance of the coastal vegetation for the production of animal life as much greater than that of the plankton; but others maintain the reverse. Brandt states, that the production of fish-flesh in a carp pond is great compared with the product of the fisheries of the North Sea per hectare; but there are so many sources of error with regard to the latter, that no great weight can be placed upon the statistics.

On p. 222 Brandt writes: »Wenn man aber den Ocean in seiner Gesamtheit im Auge fasst, so ist unzweifelhaft die Masse und damit die direkte Bedeutung der Tange, Seegräser u. s. w. sehr gering, gegenüber den winzigen Pflanzen des freien Wassers.« Brandt is most probably right here. The truth may be that in the small fresh and salt waters the coastal plants have as rule the greatest importance, but in the large, open seas the plankton, since the bottom-vegetation is quite wanting here. All seems to me to indicate, that the greatest mass of the

bottom-fauna per  $\square$  unit is to be found in the smaller waters, where the bottom-flora occurs at least in the neighbourhood, whilst the bottom of the oceans is as a rule to be regarded as waste regions (see J. Hjort and J. Murray, 1910). One thing is certain at any rate, the great, rich fisheries are not prosecuted on the open oceans, but always in more or less close proximity to the coasts or in the smaller waters.

In the paper mentioned of 1899, lastly, Brandt states in a note, that without investigations on the organisms of the coastal regions and their abundance we can easily form incorrect conclusions as to the general conditions of production in the seas, and regrets, that a method for the quantitative determination of the bottom-fauna is not known.

The Kiel investigators have thus been quite clear as to the importance of both the plankton and the benthos; it is only owing to the lack of suitable methods that the study of the latter has been pushed more and more into the background. I believe now, that we have found such a method, and I consider it as an extension of Hensen's excellent investigations, that **quantitative benthos investigations** can now also be included under the study of the metabolism of the sea.

Whilst the tendency hitherto has been too often to concentrate attention on the one side of these investigations, the aim now is to determine, what quantitative role is played in the different regions by both the plankton and benthos as food for the animal life, and in the metabolism of the sea.

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## VI. New apparatus for the quantitative collection of bottom-animals.

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The ordinary apparatus used by investigators (dredge and the like) can give some idea of the relative abundance of the animals on the sea-bottom, and on very broad lines an idea can also be gained as to whether one water has a richer animal-life than another. In the Summary to the Challenger Expedition (Part 2, pp. 1436—37) John Murray in 1895 gave such information on the animal-life in the large seas and referred to the relatively greater quantities both of species and individuals along the continental slopes. He showed for example, that the terrigenous deposits along the latter contain a much richer population than the red deep-water clay and the Globigerina ooze. Taken on the whole the sea at less depths than 50 fm. is more densely populated than all the deeper parts (p. 1433); but he is of the belief, that large quantities of continental detritus are deposited especially about the 100 fathom line, and that consequently the richest animal-life of the oceans is found here on both sides of »the Mudline«.

If however we wish to have more accurate information regarding the amount of animal-life, especially the number of individuals per unit of surface, we

must rely upon other apparatus than the dredge and trawl; with these it is difficult to say what distance they have been dragged over the bottom, nor can we know how many animals they have left behind on the distance worked over; the number is often many times more than that taken up.

A dredge was indeed originally constructed so as not to take all that lies on the bottom. The special form of dredge, from which all later dredges originated, was Otto Frederik Müller's transformed oyster dredge. An oyster dredge always has large meshes, in order just to retain the oyster and let all the mud and smaller animals pass through, otherwise it would quickly become filled with things the oyster fisherman has no desire to have; if it has smaller meshes, we can readily capture the smaller animals, but if we reduce the size of mesh to 5–10 mm. square, in order to get still smaller animals, then on soft ground, if it merely goes some few cm. down in the soil, it becomes at once filled with bottom-material.

In 1896 already I had constructed an apparatus for the quantitative determination of the animal life of the sea-bottom; this is represented in fig. 1, Plate I. It was attached to a long pole, which could reach to the bottom in the shallow Limfjord, which I especially desired to investigate. It was constructed of thin iron plates and could cut 6–8 cm. down into the bottom with its lower, sharp edges, which embraced an area of ca. 1 □ foot; the apparatus could be closed by means of a line, so that the enclosed bottom-material was dug up by the lower, movable parts of the apparatus and partially pressed up into the higher middle part of the apparatus; it was closed above by iron gauze, so that the water could escape when the bottom-material was pressed in from below. The apparatus worked very well in calm weather and in shallow water (6–8 meters); by its means I obtained the first insight into the quantity of animal-life in the Limfjord. Nothing has ever been published of this work; the main result of counting the animals collected, which were separated from the bottom-material by washing through 3 sieves of various finenesses, was that many animals were found everywhere in the Limfjord where the plaice live, and that the slow growth of the plaice in the western parts must therefore be due at least in the main to overcrowding; this was sufficient for me at that time, but later I had a great desire to investigate these conditions more closely. For this the apparatus »bottom-sampler on pole« was not satisfactory, partly because it could only be used in shallow water, and partly because the weather had to be calm.

After much experimenting one way and another I came at last to the new apparatus shown in the figures 2–3 of Plate I. This is suspended by one line and is kept open by an iron rod, which however is set free at the one end, when the lead which hangs over its centre falls down on the rod; this occurs when the line is let loose, because the apparatus has reached the bottom. Hauling on the line the two halves of the apparatus close like nippers round the bottom of the part surrounding the sharp iron edges. The water in the apparatus is pressed out through fine metal gauze on the upper side of the apparatus and makes room for the bottom-material. This bottom-sampler weighs ca. 40 kg.; by adding weights it can be made as heavy as desired. Owing to its great weight it closes with great force and the overlocking flanges make it shut very tight. It spans over ca.

0.1 m.<sup>2</sup> surface\*) and on soft bottom goes 6—10 cm. down into this. On sandy bottom it does not penetrate so deeply; but the numerous experiments made with it show, that just as it is most of our waters can be satisfactorily investigated by its means. On the other hand, it is difficult to use it on rich *Zostera* ground, or where the bottom is covered with stones or too hard shells, which it cannot crush on closing. But such stony grounds are not common on large areas. This apparatus may be used at as great depths as we wish, but as it must be used many times for an exact investigation, the difficulties increase with the depth. In our waters, however, with their shallow depths this inconvenience is as a rule not met with.

To examine 100 stations with this apparatus may take a very long time, since where there are many dead mollusc shells, these have to be carefully gone through in the sieves to find the relatively few living animals among them. Often however there is almost nothing but living animals on the bottom and in that case, by repeated washing, the bottom-material is removed and 5 samples can be taken in the sieves before the animals are counted and preserved; this method has been greatly used in the Kattegat and Baltic. In the Limfjord, on the other hand, we must as a rule be content with one sample at one time, otherwise the dead shells become so numerous in the sieves that it is almost impossible to find the living among them. I am not quite clear as to how we are to explain this shell richness in the Limfjord; but it is probably connected with the rapid renewal of the small, quickly growing molluscs, especially *Abra* and *Solen*.

In the Sound and certain places, especially in Samsø Belt and the southwestern Kattegat, I have also found large collections of dead molluscs, especially *Cyprina islandica*, *Mytilus modiolus* and other large forms; they do not grow quickly, or at any rate become much older than the small *Abra* and *Solen pellucidus*. At these places where the bottom as a rule is not soft and where the sedimentary deposits are obviously very slight owing to the strong currents, the abundance of the shells must probably be explained on the hypothesis, that the dead animals of many years lie here on the bottom without being covered by sediment. I believe that it is in this way, that we must explain for example the presence of »Skalen« at Hellebæk.

The finest sieve has openings of ca. 1.5 mm.<sup>2</sup>; naturally many small organisms pass through these, Foraminifera, young of molluscs, small worms etc.; it would be a quite impracticable work to sort out all these from the often coarse-grained bottom-material; these small animals are thus not included in the estimate of the quantity of animal life per square unit. I do not believe, however, that this error can be very great, and it is certainly of no importance, when it is a

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\*) It may be remarked here, that the bottom-sampler does not span over exactly 0.1 m.<sup>2</sup> It was originally constructed to span over a square foot, thus ca. 1346 cm.<sup>2</sup> but on the introduction of the new meter law in 1910 it was made smaller, so as to be as near as possible 0.1 m.<sup>2</sup> It has always been a little larger, however, namely ca. 1160 cm.<sup>2</sup>; all the data obtained by it are thus ca. 16% too large. At the present stage of the preliminary investigations an error of ca. 1/6th is however of but small importance. If, however, we wish to compare the results with more exact investigations in the future, then this must be taken into consideration.

question especially of determining the amount of fish-food present; the fishes do not take such small organisms, simply because they cannot see them.

The 0.1 m.<sup>2</sup> bottom-sampler, as I use it, has already passed through a long development and this is not yet ended; small improvements are constantly being made in the apparatus. I have not thought it necessary or right, therefore, to give detailed drawings of it, as it cannot well be constructed from them in any case. The accompanying photographs however give in the main a correct representation of the apparatus and its mode of working.

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## VII. Methods for the determination of the mass of animal life.

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With the help of the bottom-sampler, and the sifting and counting of the individuals of each single species in each sample, we obtain, as is shown in the accompanying charts and tables, an enumeration of the animals living on the square unit of area; but the individuals of the same species are not equally large, so that the mass of the single species is but badly represented by the number of individuals. Weighing of the individuals collected is quite necessary in order to obtain a more correct representation of their mass at each place. To obtain a view over the whole of the organic material present at a place, therefore, all species must be weighed. The rough weight of the animals, somewhat freed of water, already gives something. The molluscs are made to open by covering them with warm water, so that they let the water between the shells run out; but the other animals are weighed just as they are, though often washed with freshwater, after being rolled in blotting-paper, so as to be somewhat dry. The rough weight given in the tables has been determined in this way.

But it did not seem satisfactory to stop at the rough weight alone; on the one hand, the different animals contain different quantities of water, on the other some have such an enormous amount of calcareous matter in their shells or skeletons, that the weight of this quite dominates the amount of the true organic matter.

On the proposal of Boysen Jensen we then took up the determination of the amount of organic dry matter in the animals; regarding the methods he gives the following information.

After that the bottom-samples were passed through the sieves, as described above, the animals were either, after being weighed, preserved in alcohol, each species separately, or all the animals from a definite locality were, without being weighed, thrown together into one glass and covered with alcohol. The determination of the organic dry matter in the animals was carried out somewhat differently, according as the one or the other of these methods was used.



**1. Each species of the animals was weighed and preserved separately.**

This method was used for the following localities: Thisted Bredning, Sallingsund, the waters east of Fur, Skivefjord, Risgaards Bredning, Hvalpsund, the waters east of Venø, Oddesund, Lavbjerg Bredning, Bramsnæsvig and Isefjord.

It was determined by analysis, how much organic dry matter each single bottle contained. It was partly determined, how much there was in the alcohol by measuring its quantity and evaporating 10 or 20 ccm. to dryness and weighing the residue. It was further determined how much organic dry matter was found in the animals, by freeing them from the shells and crustaceous matter on the whole, and drying them either as a whole or a definite portion of them.

The molluscs were freed from their shells by simply picking them out with forceps. This method was also used for the small gastropods, e. g. *Acera*. On the other hand, the Echinoderms were freed of their calcareous matter by extraction with dilute hydrochloric acid and washing out with distilled water. It is naturally impossible to prevent some organic material being lost in this way; but the amount is scarcely of any importance.

The animals were first dried at 60°, until the greater part of the water had been removed, and then at 100°.

It appeared in all the determinations, that relatively large quantities of dry matter occurred in the alcohol. This was due partly to the fact, that a good deal of the salts contained in the animals are washed out in the alcohol. Now as a matter of fact, the salts do not belong to the »organic dry matter«, but it would make the method much more complicated if they were determined and deducted in each single case; I have preferred to include them therefore. As we are dealing essentially with relative values, this has scarcely any importance.

From these determinations we learn how much organic dry matter a definite rough weight of a definite species contains, and we can thus calculate the quantity of dry matter in percentage of rough weight.

The results are given in the following table:

Solen pellucidus .....	8.3	<i>Nassa reticulata</i> .....	9.6
<i>Nucula nitida</i> .....	5.3	<i>Philine aperta</i> .....	14.0
Small <i>Mya truncata</i> .....	6.6	<i>Acera bullata</i> .....	13.4
Large - - - .....	10.4	Tube-worms .....	7.1
<i>Cardium fasciatum</i> .....	7.7	Other Chætopods.....	19.9
<i>Abra alba</i> .....	8.5	Aphrodite .....	16.1
<i>Trochus cinerarius</i> .....	6.5	<i>Pectinaria</i> .....	16.0
<i>Littorina littorea</i> .....	5.1	<i>Ophioglypha</i> .....	3.8
<i>Buccinum undatum</i> .....	11.2	<i>Asterias</i> .....	7.2

The intention with these results was essentially, that they should help to lighten the work in future, as we should only require to determine the rough weight. From the percentage of dry matter we could then estimate the quantity of dry matter. These percentages for the dry matter must however be regarded as merely provisional. How much they vary in the different seasons of the year and in the different localities, has as yet been too little investigated.

**2. The species without weighing were placed together in a bottle.** This method was used in all the other cases, with the North Sea samples, a number of

the Limfjord samples, and the Kattegat and Baltic samples. The procedure in this case was as follows.

First the quantity of alcohol was measured, and the amount of dry matter it contained was determined by evaporation of 10—20 ccm. to dryness and weighing the residue.

Then the animals were sorted out and the weight of each species was determined. This weight we call the alcohol-weight. The animals here were in fact soaked in alcohol. Then a series of determinations of the dry matter was made for the animals which dominated in the sample in question. As they were different animals which dominated in the different samples, I thus obtained a series of determinations for the dry matter of all the animals occurring, and these determinations were used to calculate the quantity of dry matter of the animals which occurred in smaller quantities in a definite sample, and the weight of the dry matter of which was not directly determined.

The determinations of the dry matter were made in quite the same manner as described under 1. I may however more particularly mention the determination of the dry matter in *Echinocardium*. The digestive organs were taken out, the gut cut open and its contents washed out. Then the shells were added after extraction of the calcareous substance with hydrochloric acid. The whole was then dried and weighed.

Quantity of dry matter in percentage of the alcohol-weight was as follows:

Solen pellucidus .....	6.2	Aporrhais pes pelecani .....	6.0
Nucula nitida.....	3.0	Thracia papyracea .....	10.0
Mya truncata .....	8.2	Venus gallina .....	5.1
Cardium fasciatum .....	7.7	Astarte warhami.....	2.2
Cardium edule .....	2.4	do. borealis.....	2.2
Abra alba .....	7.0	do. sulcata .....	1.7
Mya arenaria .....	5.1	Corbula gibba.....	2.4
Leda pernula .....	5.1	Littorina.....	5.1
Macoma calcarea.....	7.6	Acera bullata .....	13.4
do. baltica .....	5.7	Philine aperta.....	14.0
Modiolaria nigra .....	6.8	Buccinum undatum.....	11.1
Mactra subtruncata.....	4.0	Chætopoda.....	10.9
Scrobicularia.....	5.4	Various worms.....	17.7
Mytilus edulis .....	2.8	Aphrodite .....	16.6
Cyprina islandica.....	3.1	Pectinaria .....	15.0
Lima loscombii .....	12.6	Echinocardium .....	1.02
Pecten pes lutrae .....	5.3	Echinus .....	2.04
Asterias .....	5.4	Diastylis.....	1.6
Ophioglypha.....	3.8	Cynthia .....	10.3
Psolus .....	21.9	Other Holothurians.....	9.1

In order to determine how many samples of the bottom-sampler are necessary in a water, to obtain an approximately correct representation of the animal life, the experiment was several times made in Thisted Bredning of

taking 100 samples distributed over the whole area outside the plant belt; on the latter I have not yet been able to make quantitative investigations, partly because this region is too shallow for the ship, partly because the apparatus is not adapted for such work. The results of the enumeration of the separate species are shown in tables I-III. It is easy to see that the number of the samples is not sufficient for the rarer animals, i. e. the larger; but it is sufficient for the smallest and more common animals. To examine into this matter more closely, the average number with its average error for each species and for each station is given in the last column of the tables I-III. These calculations have been made by Professor Johannsen's assistant, Miss J. Hempel. We see that for many of the commoner species, such as *Abra alba*, *Solen pellucidus*, *Mya truncata*, *Cardium fasciatum*, *Nucula nitida*, *Philine aperta*, *Nassa reticulata*, *Pectinaria*, worms, *Ophioglypha*, the calculations give very great exactness. Among these species we have all the principal food species of the plaice. Miss Hempel's examination has even shown that usable results can be obtained for many of these animals from 50 stations. The shortcoming in the enumeration of the individuals as a measure for their mass is the often very different size of these; we are of opinion, therefore, that better results are attained by determinations of the dry matter for each single species of the whole number found at 100 or 50 stations. From the knowledge we now have of Thisted Bredning, it will naturally contribute further to the exactness of the determinations, if the Bredning is divided into 3-5 subdivisions according to the differences present, and if we take for each subdivision a number of samples proportionate to its area, so that the samples may represent equally large areas.

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### VIII. Mass and composition of the bottom-fauna at different places in Danish waters.

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It will be seen from the Chart No. II, that the greatest rough weight or alcohol weight, including here the animals half-dried and with their shells, was found in the North Sea, namely 5368 gm. per 10 m.<sup>2</sup>, then comes a locality west of Samsø with 4406 gm.; a few places in the Limfjord have 3838 gm., 2918 gm. and 2825 gm., namely east of Venø, Thisted in the autumn, Louns Bredning and Skive Fjord. Roskilde Fjord at Roskilde has 2254 gm. The deep parts of the Sound north and south of Øresund have 1274 gm. and 894 gm., another locality west of Samsø has 1053 gm.; the Kulhus channel at the entrance to Roskilde Fjord has 1297 gm., Sprogø 709 gm. Of the remainder, the open Kattegat had 378, 284 and 427 gm., the open Baltic 170 and 80 gm.; Isefjord and Holbæk Fjord gave 444 and 269 gm. Naturally these numbers are not all sufficiently representative of the waters investigated; the localities in the North Sea, at Samsø and in Roskilde Fjord especially are too few. Regarding the details see

table VI. The results may here be regarded as endeavours to ascertain whether the apparatus and methods can be used in the different waters. For the Limfjord, the true Kattegat, the Sound, the central parts of Isefjord and the Baltic at Stevns and Møen, however, the stations are more numerous, and I believe that we can conclude from these, that of the parts investigated the Baltic is poor as regards rough weight, likewise the shallower parts of the Sound, but not the deeper; the 3 localities of the Kattegat also show fairly small values; the western Limfjord as a rule is rich. Except in the Limfjord we must have many more investigations, however, to be able to judge of the size of the rough weight for these waters as a whole. The available results give encouragement however to make further investigations; in other words the method can also be used in these waters. See also the Plates III—VI.

Consideration of the results with regard to the dry matter (see Chart No. III), in which the calcareous matter of the Molluscs and Echinoderms has been deducted, gives a somewhat different picture. The North Sea with its large quantities of *Asterias rubens* is no longer the richest locality; this is the water east of Venø with 351 gm. per 10 m.<sup>2</sup>; several other places in the Limfjord, Thisted with 282 gm. and Skive Fjord with 287 gm. come near the 286 gm. per 10 m.<sup>2</sup> of the North Sea. The one station at Samsø has 259 gm. The values for the Limfjord lie on the whole between 150—200 gm., yet the western parts in spring have only 51 gm. High quantities of dry matter were also found in the deep Sound north of Elsinore, 174 gm.; but the open Kattegat has but small values, 20—49 gm., the Baltic even smaller 8—15 gm. The Isefjord shows varying values from 23—110 gm.

That the Baltic in the part lying between Rügen and Denmark will really show small quantities of bottom-animals on further investigation, I do not doubt, nor that large parts of the Kattegat are moderately populated and that the Limfjord has on the whole a greater population; but in these regards we can hardly conclude more from these investigations at their present stage.

The locality which excluding the Baltic gives the smallest quantity of dry matter, namely 0.5 gm. per m.<sup>2</sup>, is the white clean sand in the Sound at a depth of ca. 2 meters; its rough weight however was 17.7 gm. per m.<sup>2</sup> This is the only locality investigated which lies near the coast and from a topographical standpoint is related to the localities investigated by Fried. Dahl in 1893 in the mouth of the Elbe; per m.<sup>2</sup> he sometimes found quantities of Gammarids up to over 1000 in addition to usually small Molluscs and worms, but his one case of a large quantity was 47.4 cm.<sup>3</sup>, otherwise the mass was but 7.3 cm.<sup>3</sup> down to almost nothing; results which show, that the shallow, sandy coasts in spite of their great richness at certain times of the year, mostly of small animals, are yet far from equalling the deeper parts especially of fjords. I may mention here the interesting observation of Dahl, p. 183, that at Dahme in the Baltic he found many Crustacea in August 1890, but in December 1889 at exactly the same spot he found no animals at all.

A rapid inspection of the tables V and VI will show, however, that there is on the whole several quite characteristic differences between the fauna in the deeper parts of the Kattegat with the Belts and the fauna in the fjords and especially

in the Limfjord. One of these differences consists in the large mass of Echinoderms, which is found outside the fjords. The numbers of *Ophioglypha* are certainly large in the Limfjord, but even though they belong to the species *O. texturata*, the numbers are yet so small that their rough weight at several places is less than that of the comparatively rare *Asterias rubens*. In Nissum Bredning *Echinocardium cordatum* occurs in large quantity; this region forms a transition to what we meet with outside the fjords. On the areas investigated in the Limfjord the remaining Echinoderms are essentially of no importance; the result would certainly have been different if the *Zostera* belt had been included in the investigations, as *Echinus miliaris* among others is common there. In Thisted Bredning the rough weight of the Echinoderms only amounts to a few per cent. of the whole rough weight, in Kaas Bredning somewhat similar, in Nissum Bredning on the other hand, the rough weight of the Echinoderms amounts to more than half of the whole animal life present. I may just recall here, that in the sample from the North Sea (Table VI) just off Nissum Bredning, the Echinoderms there, *Ophioglypha*, *Echinocardium* and *Asterias*, the same three which are so common in Nissum Bredning, amount to almost  $\frac{6}{7}$ ths of the total present (alcohol weight). It was here *Asterias* which lived well at the expense of the numerous *Maetra subtruncata*, as evidenced by the numerous empty, but still connected shells of this Mollusc. We may hope that the conditions are not so unequal everywhere in the North Sea. In the northern part of the Sound and W. N. W. of Kullen we investigated 3 localities in deep water (Table VI); they show a quantity of Echinoderms whose alcohol weight is approximately equal to or more than half of the total animal life; here *Echinocardium*, *Echinus drøbachiensis* and *Psolus phantapus* as also various Ophiuroids especially are abundant. I remember distinctly, that during the time I was making collections onboard the Gunboat »Hauch« in the Kattegat, the Echinoderms at many localities in deep water in the Kattegat were the animals which filled the most; I was thus obliged to learn how to distinguish the species of this group, so that I could note their occurrence in the journals and then throw them overboard; to keep them all in bottles as I did with the smaller species of animals was quite impossible. There is no doubt, that Echinoderms both in volume and weight are exceedingly abundant at many localities in the deep Kattegat, in the Belt Sea at Samsø and in the northern and deep parts of the Sound. In the fjords and in the shallow water outside them, on the other hand, they are as a rule of much less importance in comparison with the remaining animal life present.

A second difference which appears from our investigations is the great masses of large Lamellibranchs and large gastropods, which are found in almost the same localities as the large Echinoderms. I may mention *Cyprina islandica*, *Macoma calcarea*, *Mytilus modiolus*, *Pecten pes lutrae* and *Aporrhais pes pelecani*. *Neptunea antiqua* and *Buccinum undatum* are only mentioned a few times in the Tables, yet also belong to the characteristic forms of these regions. Taken on the whole, we have only to cast a glance at the large collections made with the bottom-sampler in the deeper parts of the Kattegat and the northern Belt Sea, to be struck by the quantity of large Echinoderms and large Lamellibranchs, which occur there. Collections in shallow water and especially in certain regions

of the fjords give a much greater mass of small animals and less of the large.

From this there are exceptions, however, especially in the almost enclosed fjords. I may mention, for example, that *Mya arenaria* is quite predominant at certain places in Roskilde Fjord off Roskilde (see Table VI), that *Scrobicularia plana* is the same in the northern narrow part of Roskilde Fjord (see Table VI), but I have not found anything similar in the true Isefjord or inside Ourø (see Table VI).

In certain parts of the Limfjord a few large Lamellibranchs also predominate, thus *Mya truncata* in Thisted Bredning (see Table V); the same applies to certain, especially easterly parts of Livø Bredning and Skive Fjord (see Table V), and lastly, both *Mya truncata* and *Mya arenaria* appear at places in great quantity in the innermost part of Louns Bredning. But at most of these places in the Limfjord there also occur a quantity of small animals, and in the regions between Nykøbing and Oddesund the latter dominate. I shall return to this subject in a later section.

Tables V and VI show how little the whole group of Crustacea is of importance, both in number and weight, everywhere at the places investigated, and yet I cannot believe that the smaller Crustacea could escape the bottom-sampler; it is rather due to the fact, that so few samples were taken in the plant region. On the other hand the groups of worms are richly represented in both respects; *Aphrodite* and *Pectinaria* are very abundant, and also a number of other Chætopods, which however I have not yet determined to their species.

At one place only, in Nissum Bredning, a Holothurian (*Ascidella aspersa*) is found in large quantities, larger in autumn than in spring; but they are so numerous here in the autumn, that trawling along the bottom is almost made impossible by them.

Even *Amphioxus lanceolatus* has been taken with the bottom-sampler in the Kattegat (see Table VI), 5 specimens in all; but otherwise none of the higher animals. The Tables will show, however, what has been taken and what is wanting in these collections. I may just mention one more thing, the large quantity of *Astarte warhami*, *A. borealis* and *A. sulcata* at Sprogø; their rough weight is greater than the half part of all the animals found. In earlier works I have drawn attention to the occurrence of these characteristic Molluscs far into our waters; but I did not know that their quantity was so enormous.

It is evident, that except for the Limfjord we have as yet far too few investigations of this kind, to be able to estimate the mass of the single species in the waters investigated as a whole; and even in the Limfjord it is only in Thisted and Nissum, and perhaps in Kaas Bredninger, that such can be done — for some of the species; but even if this must be done with a certain reservation, as the plant belts have not yet been investigated, yet several conclusions may be drawn from the numbers found regarding the relative proportions of the different species; see further a later section.

The Plates III—VI have been drawn to depict the sea-bottom in various waters; to these and their explanation reference may be made here.

## IX. The annual production in general.

What the Tables directly show with regard to the mass of animal life per square unit of area, refers only to the mass of animals present at a given time; but what I specially wish to know is, how great is the quantity of organic dry matter which each species produces each year per square unit at the different places, thus the annual production; this would give the best information regarding the amount of food which is annually available.

If we could compare the mass of the animal species, for example in the autumn, with the quantity of corn which is still unreaped on a corn-field, and could consider everything present as the year's production, the matter would be simple enough; but it is much more complicated for the sea-bottom. The quantities of dry matter found do not for example all grow up in one year or less, as in the case of the corn; some part does it is true, but others are several years old, such as the mass of the large Echinoderms, large Lamellibranchs and Gastropods. When we know the age of the different animals, we can distinguish the one-year old of rapid growth and the old, and by excluding these we can obtain some insight into the annual production for some species at least. Thus, in the Limfjord in the autumn we might be able to calculate the quantity present of *Abra*, *Pectinaria*, many other worms, in part *Solen pellucidus*, young *Mya* etc., to obtain the production of the year; in the Kattegat however we must exclude from the year's production most of the large *Cyprina*, *Modiola* and others, as also the large Echinoderms. These last contain further so little organic dry matter, when the calcareous matter is deducted, that they are on the whole of practically no importance as food producers. But if we included the small, young, quickly growing Lamellibranchs in the Tables for the whole year's production in the Limfjord we should make a great error; since in autumn the quantity of for example *Abra* is certainly greater than in spring, which is connected with their birth in spring and their rapid growth in summer, but during the whole of this time, as soon as they have reached a suitable size, they have been exposed to the attacks of plaice, eel and other fish, *Asterias*, perhaps *Buccinum* and other animals; we should therefore make too small an estimate, if we took the autumn increment to represent the whole production of the year.

We cannot attain therefore to more than an idea of the annual production of a bottom-fauna for the present; but on the basis of our study of the age of the animals, growth-rings on the shells of the Lamellibranchs, the rapidity with which a species grows up from spring to autumn etc., we can obtain a better estimate. For example, I have investigated Nissum Bredning with large trawls for many years every spring and every autumn, and seen that such enormous quantities of *Ascidella aspersa* occur every autumn, whilst scarcely any are found in spring, that the annual production in its case must certainly be enormous. This can also be seen from the numbers in Table V.

In late summer *Proto ventricosa* appears on the *Zostera* in our fjords in such quantities, that every net used here is at once filled with these animals and to such a degree that every single mesh is jammed with them, and the whole net

looks as if it were alive. In the spring we must search keenly to find any *Proto* at the same places. Boats placed clean in the water in the spring are in a short time covered with *Balan* and *Mytilus*, and all wood-work which is not very thick, is pierced in the course of a summer by *Teredo* and *Limnoria*. *Clavellina lepadiformis* literally »flowers« in enormous masses in the summer and disappears again in the autumn, to hibernate as small, grayish crusts. Something similar happens to *Aurelia* and *Cyanea*.

The whole of the animal life on the *Zostera* is essentially a summer phenomenon. *Rissoa*, *Cerithium*, *Trochus*, *Lacuna* etc., certainly hibernate among its roots; it is only late in the year that they crawl up to feed and spawn, and the water is then full of their young. Certain *Actiniae*, the Nudibranchs and hydroids first appear late in the summer; briefly, wherever our eyes can see it, there is an enormous annual production in our fjords from spring to autumn. We could also say the same of the vegetation here (Rosenvinge). It has taken me a long time, to get my eyes opened to this great production in our fjords from spring to autumn; most of it is indeed hidden under water. Our fjord fisheries follow this pulsation of the year, in the case of the eel, plaice and other flat-fishes; in the main they yield only what is gained in growth from spring to autumn; thus the fisheries in the fjords are of little account in the spring but rich in the autumn, until all that can be used is fished up or emigrate; the fishermen must then wait, until a new growth has taken place in the course of the next summer.

Briefly then there is a large annual production in the fjords, and our Tables also show high values for several species in the autumn. On the other hand, what the increment may be in deep and large waters such as for example in the Kattegat and Belt Sea, we do not know; only exact, quantitative determinations will be able to show this; what I have seen hitherto with regard to the deeper waters, has given me the impression, that the fauna here does not change with the seasons to any obvious extent, — nor is it reasonable to assume beforehand, that such does happen.\*)

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## X. Producers and consumers in the Limfjord in 1909—1910.

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The animals best represented in Table V are those which live on detritus and plants, thus the producers; but a large and specially important group of consumers, namely the fishes, are quite wanting, partly owing to

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\*) I may refer here to a recently published work by V. Franz: Ueber die Ernährungsweise einiger Nordseefische, besonders der Scholle. (Wiss. Meeresunt., IX Bd., Hefte 2, Helgoland 1910). F. is of the opinion, that we cannot possibly assume, that more plaice food is found in the North Sea at certain, definite seasons than at others, and bases his views on the fact, that most of the animals the plaice feeds on, live for several years.



their size, and lastly owing to the swiftness with which they can escape from such a small apparatus as a 0,1 m.<sup>2</sup> bottom-sampler. We have therefore only the data of the fisheries statistics to rely upon. But with the help of these we can only ascertain what is caught yearly, not what lives, in this water.\*) I will therefore only count with round numbers in the case of the fishes. An exception may be made however for the plaice, regarding which specially detailed data are kept owing to the extensive transplantation of this fish; but the data have other shortcomings, such as that they do not include the plaice destroyed by the whelks, and this amounts perhaps to a third of the whole year's catch. In order to counterbalance this defect, I have not deducted from the production, that the plaice when transplanted weigh ca. 7—10 kg. per 100, nor that other flat-fishes such as flounder, dabs, turbot, are included in the statistics; even then the statistics certainly show a smaller quantity than the catch actually has been.

According to the fisheries statistics the following quantities of fish were taken in Thisted Bredning in 1908 and 1909:

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This would in part agree very well with my view, if it really is the case; but the foundation of Franz' conclusion leaves a great deal wanting. Applied for example to a stock of partridges regularly kept down by shooting, it would not hold good, in spite of the fact that the pheasants live for several years. Most of them do not do so however; as the 0-group of the autumn, which is for the most part shot down, is much in excess in most years. I may take an even closer example *Abra alba*, which both in the Limfjord and in the North Sea (according to Franz) has so great importance for the plaice; he states that it may live until it is 5 years old to judge from the growth-rings on the shells. In the Limfjord it only lives 2 years, at least I have not been able to find any older, and these are even very seldom, on the soft bottom at any rate. Now it is just this species which in the Limfjord is so abundant in the autumn in contrast to the spring (see Table V); its 0 group is prodigiously numerous in the autumn. It is of course possible, that it often only becomes 1 to 2 years old in the Limfjord, owing to its being much sought after by the fish, and may become older in the North Sea; but in that case its autumn group in the latter should show a maximum. We must have accurate information regarding this.

In the Kattegat I have seen a similar, extremely numerous 0 group of *Mactra subtruncata*, which appears at certain places near the coast in autumn and which is eaten with great avidity by the plaice living there. This species also lives for several years, but it is certainly much more numerous at certain seasons of the year than at others. I should think it very probable that, on the shallower stretches of the North Sea, especially along the Schleswig and Jutland coasts, similar numerous 0-groups of the Lamellibranchs living there and perhaps of other animals appear in the autumn.

F. mentions *Solen pellucidus*, *Corbula gibba*, *Pectinaria* and other species, which however are not important in the Limfjord; in *Pectinaria* I know there is also an enormous autumn group in the Limfjord, but not in *Corbula* and probably not in *Solen*. As said, I am much inclined to believe, that the North Sea as a whole does not have such great changes in the quantity of food with the seasons, but I would only advise against concluding that this is the case on the basis of the above reasoning.

\*) In Nissum Bredning, where the plaice is so extremely numerous, I have endeavoured to capture them with a 1,2 m.<sup>2</sup> bottom-sampler, and thus to determine their number; but though several plaice were caught with this apparatus, the accuracy is not sufficiently great. Such experiments are however being continued and will eventually succeed I hope. The watchfulness of the plaice is the greatest hindrance to an enumeration.

	1908	1909	Average	Dry matter in kg.
Herring..... Ol (80)	1,400	2,000	1,700	>
Eel..... kg.	47,200	24,000	35,600	17,800
Plaice..... >	75,000	81,000	78,000	19,500
Cod..... >	52,500	47,500	50,000	10,000
Lobster..... >	550	325	>	>
Prawns..... >	3,500	500	>	>
Various..... >	550	350	>	>

or ca. 50,000 kg. dry matter on an area of 11,843 Tdr. land (1 Tdr. = 1.4 acres) or about 65 million m.<sup>2</sup>

The percentage of dry matter in the fishes varies somewhat according to their condition; from experiments made by Boysen Jensen the percentage of dry matter for the plaice is about 25 %, cod 20 %, the eel varying from 28.6 to 60.7 %, here taken at 50 %. The quantities of the remaining animals captured are so small, that I have taken no regard for them at all in the calculation in round numbers. The quantity of dry matter for the eel, cod and plaice caught in Thisted Bredning on an area of 65 million m.<sup>2</sup> was ca. 50,000 kg. or about 0.77 gm. per m.<sup>2</sup>; thus 7.7 gm. per 10 m.<sup>2</sup> This value may now be compared directly with the numbers given for the dry matter of the lower animals in Table V.

First of all, however, some information may be given with regard to what has been found in the stomachs of the different fish species in Thisted Bredning.

In the cod: *Buccinum* (soft parts and opercula), *Idothea*, *Proto ventricosa*, *Stenorhynchus*, *Crangon*, *Aphrodite*, Nemertines (?), *Mya truncata*, *Solen*, *Abra*, *Actinia* and *Gobius*.

In the eel: *Acera*, *Philine*, *Cerithium*, *Solen*, *Cardium*, *Nucula*, *Pectinaria*, *Nereida*, *Priapulid*, Nemertines(?) and *Idothea*.

In the plaice: *Mya truncata*, *Abra alba*, *Solen pellucidus*, *Cardium fasciatum*, *Nucula nitida*, *Corbula gibba*, *Pectinaria*, *Chaetopoda*, a few times *Ophioglypha* and very seldom *Acera bullata*, *Asterias rubens*, *Philine*, *Tellina baltica*, *Crangon*, *Diastylis*, *Gammaridae*, *Aphrodite*. The first 8 far exceed the last mentioned. In addition to the *Chaetopoda* it is especially young *Mya*, *Abra*, *Solen* and *Cardium* which are by a long way the commonest food animals.

As will be seen, a number of the fishes seek their food in the plant belt, most of the Crustacea are taken there, as *Idothea*, *Proto* and *Stenorhynchus*, and the eel and especially the cod certainly find a part of their food there; both are very fond also of making hunting expeditions in here, whilst the flat-fishes come here but seldom. The cod certainly feeds also on many gobies and other fishes and *Buccinum*; it is certainly not so closely bound to the soft bottom as the eel and plaice.

I would thus refer only the eel and the plaice to the fishes, which find their food among the smaller animals of the soft bottom-soil, but even if we include the cod here with its 10,000 kg. dry matter, it is not much compared with the total quantity for the eel and plaice, namely ca. 40,000 kg. of dry matter, or 6.2 gm. per 10 m.

Comparing now this 6.2 gm. of fish dry matter with the quantity of dry matter contained in the animals these fish feed on, as shown by Table V, we see

that *Abra* in autumn of 1910 alone has a larger quantity of dry matter, namely 9.51 gm., the other small Lamellibranchs 5.51 gm., all the worms together 9.42 gm.; all these small animals thus have a total quantity of dry matter of 24.5 gm. In the spring of 1910 the quantity of the above-mentioned animals was somewhat less. The young *Mya* are not all included here.

Such momentary pictures of the fauna thus show, that the quantity of the food-animals is quite considerable, at any rate compared with the quantity of fish caught; we shall return to this matter later.

In Table V however we find among the lower animals several, which like the fishes must also be referred to the consumers, namely *Buccinum*, *Nassa* and *Asterias*.

*Echinus miliaris* belongs in reality to the *Zostera* belt, which, as the Chart shows, extends somewhat out into the region investigated with quite a slight *Zostera* vegetation; *Ophioglypha* probably is partly worm and partly detritus feeder. With regard to *Asterias rubens*, this is present in such small numbers in the Table, that we cannot conclude anything as to its real abundance in the Bredning; it is an eager devourer of Lamellibranchs, and in an aquarium eats up an extremely large number of these in a short time.

With regard to *Buccinum*, I have endeavoured in another way, by diving and by using a larger bottom-sampler, to determine the quantity in 1909 somewhat more precisely (see Report XIX, 1911), and then found that 1.3 *Buccinum* lived on each m.<sup>2</sup>, thus in all ca. 20,000 barrels of 95 kg. each or 1,900,000 kg. rough weight, or ca. 30 gm. rough weight per m.<sup>2</sup>. If we use the percentage of dry matter 11.62 Boysen Jensen found in the spring, Rørdam in the winter found 15.1%, we have 3.486 gm. dry matter, the shells not included, per m.<sup>2</sup>, or 34.86 gm. per 10 m.<sup>2</sup>, thus 5 times more than the Table shows.

The quantity of dry matter for *Nassa* is seen from the Table V to be on an average 3.57 gm. per 10 m.<sup>2</sup>; it must be considered to be much better represented in the Table than *Buccinum*, as it is much more numerous. In the great whelk fishery we carried out, the mass of *Nassa* was much less than that of *Buccinum*, so that there can be no doubt, that the mass of *Buccinum* is in reality much greater than that of *Nassa*.

The quantity of dry matter in these whelks is, as shown by the foregoing, much greater than the quantity of dry matter in the fish caught; the latter was only ca. 7.7 gm. per 10 m.<sup>2</sup>. Although the fish caught do not represent all there is of fish-flesh in the Bredning especially eel, for example, of which there are many younger year-groups, yet we may assume, that the dry matter of the whelks is much greater in quantity than the quantity of dry matter in the fishes.

If these large whelks and *Asterias* lived on the same small animals as the eel and plaice live on, it would be an awkward thing for the rational fishery in Thisted Bredning; they do not do so, however, at least not exclusively; we know, how eagerly the whelks attack almost all fish in the summer which they can get hold of, and all oysters which are open; but what they normally live on, we do not know, as it was only when something eatable had been given them, that I could find anything determinable in the stomachs of the whelks; probably they can also overpower large Lamellibranchs; but they can obviously go hungry for a

long time; in his paper cited Cotton mentions that whelks go without food for a long time. I am inclined to believe, that a very essential part of their food comes from the large Lamellibranchs (*Ostrea*, *Cyprina*, *Modiola*, *Mytilus*, *Tapes*), which owing to their relatively small numbers are only seldom mentioned in the Tables; they cannot always open these Lamellibranchs perhaps, before the latter die; but then they evidently fall a prey to the whelks; and it is certain that these Lamellibranchs die in large number, as is witnessed by the many empty *Mya* shells with hanging siphons, and the many fresh, connected oyster shells without any growths on them.

Whilst these large Lamellibranchs as detritus-feeders must be included among the producers, they are of but little importance when adult as fish food. Only the young *Mya* are at certain times so numerous, that they are of importance — even considerable — in this regard; but in general the large Lamellibranchs in connection with the fishes must be regarded as a separate, indifferent group of producers.

Lack of information regarding the normal food-animals of the whelk is a great want in this investigation; this will, it is hoped, be removed in the future.

So far as the cod is concerned, on the other hand, *Buccinum* is to be regarded as a producer of great value; but the cod is not always an abundant guest in these waters; it is for this reason probably that *Buccinum* is so common in certain years.

Whilst *Buccinum* and *Nassa* by attacking the captured fish are direct competitors of the fishes, I cannot therefore accuse them of being food-competitors of the fishes; they may perhaps even be of importance as scavengers, as I take it for granted that almost all animals of the larger kind end as food for fishes or whelks. The Echinoderms however form in the main an exception; they are but seldom eaten in the Limfjord; they probably end as food for the bacteria.

If it is thus difficult to determine in all cases, owing to insufficient biological investigations, what animals are producers and what consumers, it is even more difficult to determine, how much the various animals produce and consume. The quantity of dry matter of all the animals together seems indeed to vary somewhat in Thisted Bredning from one year to another or from spring to autumn, but at no time is it very small; these variations evidently show only for a small part, what is produced and again used up in the course of the year.

From a consideration of the mass of the separate species at different times, we can on the other hand obtain good information regarding the annual production, in a similar manner as Hensen (1887, p. 95) in part determined the production of plankton; in this way, however, we only obtain minimum values.

*Abra alba* in Table V shows, for example, an increase from spring to autumn 1910 of 9.54 gm. per 10 m.<sup>2</sup>; the whole of this can be credited to the annual production. In the same period *Nucula* and *Pectinaria* show an increase of together 2—3 gm. per 10 m.<sup>2</sup>; but *Solen*, *Cardium* and several others of the food-animals of the fishes show a decrease; naturally, not because these rapidly growing animals have not produced anything at this time, but because they are sought after so much. From the autumn of 1909 to the autumn of 1910 *Mya* shows an increase of no less than 163 gm. per 10 m.<sup>2</sup> According to this mode of

calculating, the production for all the animals in Thisted Bredning mounts up to 200 gm. of dry matter per 10 m.<sup>2</sup> per annum. To get a nearer approximation we must know exactly the growth and age of the separate animals; the large *Cyprina*, *Buccinum* and *Nassa* evidently grow slowly; of *Asterias* and *Ophioglypha* too little is known in this regard. It is remarkable, that the numbers of *Ophioglypha* have been steadily and greatly decreasing from 1909 to 1910.

Only Nissum Bredning in addition to Thisted has been so carefully investigated, that we can in any way judge as to the abundance of the food-animals; a comparison of the two is therefore of interest. *Mya truncata* has not been found at all in Nissum Bredning, but here *Ascidella* and *Echinocardium* are numerous especially in the autumn. The total quantity of dry matter in Nissum Bredning was 50.58 gm. per m.<sup>2</sup> in the spring, 123.18 gm. in the autumn; thus, in spite of the many Holothurians and Echinoderms not half of what it was in Thisted Bredning (see Table V); but the fluctuation points to a fairly large annual production, namely of at least 72 gm. per 10 m.<sup>2</sup>; as shown in Table V, this is due specially to the increase of *Ascidella*, but in smaller degree also of other animals.

Thus we do not come in general to any very definite results in endeavouring to determine the production of the single species in Table V by means of their annual increase; much of it disappears owing to the efforts of fishes and other animals. I have endeavoured, therefore, always in principle in the same manner as Hensen, to determine how much the fishes in these waters annually devour. This amount which is eaten by fishes and other animals, must be added to the increase from spring to autumn, which is shown in Table V, in order to obtain an insight into the total production of the bottom-animals per annum.

To be able to make such a calculation we must know, what quantities of food, for example, a plaice takes per day and per year, and I have long sought after a method of obtaining information on this point. I have thought of feeding the plaice in captivity, but soon gave up this idea as I foresaw that it would give far too uncertain results, which further would throw no light on the natural conditions in the open. I have endeavoured to catch the plaice with full stomachs and intestines and keep them in a well, until the contents were digested, so as to determine the time the process took; but the results from this were far too irregular; the plaice are easily damaged especially when the stomach and intestines are full of Lamellibranchs. I then came to the idea of catching the plaice at different times of the 24 hours, so as to see whether there was a difference in the quantity of food by night and by day, and thus if possible obtain some information regarding the quantity of food per 24 hours, and this method soon proved itself useful. I shall return to this below, but may mention here, that V. Franz in his work published in 1910, which I became acquainted with later, has made similar experiments to determine the food-capacities of the plaice at different times of the 24 hours in the North Sea, but he has not found that the digestive tract is emptied so completely as I have found in some of my experiments; perhaps because the plaice in the North Sea feed at night-time on the luminous *Amphiura filiformis*, which does not live in the Limfjord, but perhaps

because he did not choose the right times in the course of the 24 hours; thus for the large plaice he does not state any definite hour but simply »abends« or »morgens«, and the investigations were not made in the same 24 hours. He comes however to the result, that the plaice is a »Tagfresserin« as a rule (*-Amphiura*), and that it empties its digestive tract in the course of at most 24 hours. This agrees with my observations at certain places in the Limfjord.

To investigate whether the quantity in the digestive tract was connected with the times of the day and night, a number of plaice which we ourselves had taken by trawl at Glyngør at different times of the 24 hours, were examined on 22. and 23. August. The result is shown in the accompanying table.

Plaice from Glyngør. 1910.	22. Aug. 25 Individ. 10 a. m.	23 Aug. 25 Individ. 4-5 a. m.	23. Aug. 20 Individ. 8 a. m.	23. Aug. 12 Individ. 2 p. m.	23. Aug. 40 Individ. 7½ p. m.
Full stomachs and gut.....	20	1	Very little in stomach and gut.	7	33
Full stomachs and empty gut .....	3	0		0	1
Empty stomachs and full gut.....	1	0		4	2
Empty stomachs and empty gut .....	1	14		1	2
A little in rectum .	0	10		0	2

Thus, in the early morning most of them had empty tracts, but at 10 a. m. most were filled up, as also in the afternoon and evening till 7 p. m. This roused the desire to continue with these investigations, and they were carried out in the next following days in Nissum and Thisted Bredning, with a slightly different subdivision of the contents of the digestive tract. The result is seen in the accompanying table.

Plaice taken in Nissum Bredning, August 1910.

Date.	6 Kilo. Kl.	No.	M	T	M	T	M	T	M	T	M	T	M	T	M	T	M	T
			t	t	l	t	f	t	f	l	l	l	l	f	t	l	t	f
25.	2½ p. m.	64	2	2	0	3	2	6	4	12	33							
25.	8-10 p. m.	53	—	—	—	1	4	3	12	6	27							
26.	4-6 a. m.	65	17	10	3	—	16	2	16	1	—							
26.	8-11 a. m.	57	—	—	1	7	4	5	1	2	37							

Plaice taken in Thisted Bredning, August 1910.

Date.	24 Pd. Pd.	No.	M	T	M	T	M	T	M	T	M	T	M	T
			t	t	l	t	f	t	f	l	l	f	t	f
29.	11½ p. m.	39	—	—	—	—	—	2	1	—	36			
29.	2½ p. m.	35	—	—	—	—	—	1	—	—	34			
29.	8 p. m.	34	—	—	—	1	—	1	—	—	32			
30.	5 a. m.	43	17	19	2	—	3	—	2	—	—			

M = stomach, T = gut, f = full, t = empty, l = a little.

The results from Sallingsund and Thisted Bredning seem to me sufficiently clear; the digestive tract is emptied of its contents before 4—5 a. m. and is again filled in the course of the forenoon; in Nissum Bredning on the other hand the morning investigation at 4—6 a. m. shows a little in the gut and stomach; this suggests a longer time for digestion in this Bredning, where the plaice thrive very badly (cf. Franz for the North Sea). Whether the plaice digest much in the course of the day, is not known; but what is found in the digestive tract, when it is full, is digested in the course of the day at any rate in Sallingsund and Thisted Bredning; this is therefore its minimum of food at this time of the year.

To ascertain something about the mass of this minimum, the amount of dry matter in the stomach-contents of 6 kg. of plaice from Thisted and Nissum Bredning was investigated, partly taken when they contained least, partly when they had most food; but as it is impossible to separate out the Lammellibranch shells in the finely divided contents of the stomach, Boysen Jensen determined the amount of carbon in these; when the results are multiplied by 2, we may assume that we are near the actual quantity of dry matter in the contents of the stomachs; but larger or smaller parts of the food there must be considered to have been digested and absorbed.

		organic dry matter
Thisted Bredning,	$\frac{29}{8}$ 1910. 4—5 a. m. 6 kg., 22 spec.	3.42 gm.
— — ,	$\frac{29}{8}$ 1910. 11 $\frac{1}{2}$ a. m. 6 kg., 19 spec.	18 gm.
Nissum Bredning,	$\frac{26}{8}$ 1910. 4—6 a. m. 6 kg., 65 spec.	4.4 gm.
— — ,	$\frac{26}{8}$ 1910. 9—11 a. m. 6 kg., 57 spec.	8.4 gm.

I believe that we get nearest to the real conditions for Thisted Bredning, if we assume that the plaice digest daily at least as much as they have at any one time in their digestive tract; thus, the 19 plaice consume ca. 18 gm. daily, or almost a gram for each, which means 10 gm. raw matter daily or 3 gm. dry matter per kg. daily. As about 100,000 kg. of plaice was fished in Thisted Bredning in 1910, the amount they have eaten, provided that they eat just as much from April to November or 240 days of the year, would be 72,000 kg. This estimate however is probably too high, as the plaice are small in the beginning and only later eat much, especially in August to November.

As already mentioned we know approximately the number of plaice which live each year in the Bredning; almost all in fact are transplanted and by far the greater part are fished up each year before Christmas. Here, therefore, we are dealing with a yearly growth and the conditions are thus much simpler than they usually are in the sea. It is different on the other hand with the eel; we only know roughly how many are fished yearly, but I imagine that a very large number migrate out as silver eels without being fished in the Bredning; further there are at least 6—8 younger age-groups which are yet too small to be caught. In this case a calculation of what the quantity of eels fished has eaten in a year, is far from giving the amount annually devoured by all the eels; it is evident, therefore, that one kg. of eels is much dearer to produce than one kg. of plaice, even if we presuppose that both eat about the same amount per kg. per annum and grow to an equal extent.

If we estimate that every plaice in Thisted Bredning eats 10 gm. daily for ca. 240 days in the year, this gives a rough weight of ca. 2400 gm. per annum; as the plaice in 1910 increased on an average 375 gm. from April to November, this gives an increment which is about  $\frac{1}{6}$ th of the rough weight of the food consumed, a figure which agrees very well with the amount eaten by fishes reared in a pond. The ca. 360,000 transplanted plaice would, with a gm. per day, eat ca. 86,000 kg. dry matter annually; but as most of them are caught before they have been in the Bredning 8 months, this figure is certainly too high. Taking the monthly statistics in account among other things, I should imagine that ca. 50,000 kg. of dry matter would correspond better to the annual consumption of the plaice in Thisted Bredning. This gives for each of the 65 million m.<sup>2</sup> in this Bredning a production of 0.77 gm. per m.<sup>2</sup> or 7.7 gm. per 10 m.<sup>2</sup> If we assume that the eels, both young and old, eat twice as much, the total consumption of these two species would be ca. 23.1 gm. per 10 m.<sup>2</sup> annually; thus in reality not a great amount by comparison with the annual production of dry matter of up to 200 gm. per 10 m.<sup>2</sup> The connection of *Mya* with this will be discussed later.

In Nissum Bredning, where the plaice does not digest the contents of its stomach each day, the residue of 4.4 gm. in the morning must be deducted from the total evening contents of 8.4 gm., so that ca. 60 plaice here per day only eat 4 gm. in all, or 0.067 gm. per individual. Now we know from the investigations of many years (see e. g. Report XVIII 1909 Table C), that there are at least 40—60 times as many plaice per □-unit of area in Nissum as in Thisted Bredning; as each plaice in the former eats ca. 0.067 gm. day, ca. 50 plaice would devour  $50 \times 0.067$  gm. or 3.35 gm. on the same area, where one plaice in Thisted Bredning eats 1 gm.; in other words, 3.35 times more plaice food is used per m.<sup>2</sup> in Nissum Bredning than in Thisted Bredning; thus annually  $3.35 \times 7.7$  gm. or 25.8 gm. per 10 m.<sup>2</sup> against 7.7 gm. in Thisted Bredning.

The food consumption of the plaice in Nissum Bredning is thus much greater than the calculated amount of the food of the plaice and eel together in Thisted Bredning (23 gm. per 10 m.<sup>2</sup>). This result is not surprising, when we know that in Nissum Bredning outside the 6 meter line practically no other animals are found at all times but the plaice; here whatever is eaten, is eaten by the plaice.

It is not my intention, naturally, that too much weight should be attached to these figures and the results of the calculations; they should rather be regarded as a first experiment in breaking a way where hitherto any calculation or even an estimate based on figures, measure and weight, has been impossible; that the preliminary results obtained are so reasonable as they are, has in fact surprised me, but they also encourage the hope of obtaining even better in the future; in any case they have been able to show, that the plaice in Nissum Bredning really eat less per individual than in Thisted Bredning, and we can thus understand their small annual growth in Nissum Bredning. There is certainly overcrowding in the latter; but no little food is produced on the bottom per m.<sup>2</sup> though certainly less than in the central Limfjord.

There is therefore evidently a limit to the extent we can carry on the transplantation of the plaice; the density may be too great; where this limit lies, is for future investigations to determine. We shall probably hardly be able to find



it by way of calculation, as it is difficult to determine, how much is produced annually of plaice-food per m.<sup>2</sup>; direct practical experiments with transplantation of more and more plaice per hectare will however lead to the goal, namely, slower growth; but it will only be by means of similar studies to the present, carried out at the same time, that we shall learn whether this slow growth is really due to the insufficient quantity of the food-animals or possibly to other causes. It is remarkable, that the plaice in Nissum Bredning do not eat up everything there; as it seems to me that they must always be hungry. The reason is possibly, that they cannot find all the animals which might serve them as food.

In Nissum Bredning the plaice in 1910 were feeding especially on *Nucula* and *Macoma baltica*, *Abra*, *Mactra*, *Philine*, *Pectinaria* and worms, as also more rarely *Corbula*, *Solen*, *Acera*, *Idothea* and *Ophioglypha*.

Comparing the quantity of the animals the plaice eats, in both Bredninger, we obtain for Thisted Bredning, excluding *Mya*:

1910. Spring 19.03 gm. Autumn 24.00 gm. per 10 m.<sup>2</sup>

For Nissum Bredning:

1910. Spring 7.49 gm. Autumn 13.10 gm. per 10 m.<sup>2</sup>

The increment from spring to autumn is due in Thisted Bredning mainly to *Abra alba*, in Nissum Bredning on the other hand to *Nucula*, *Pectinaria* and *Aphrodite*. At all times of the year, therefore, there is more plaice-food per m.<sup>2</sup> in Thisted Bredning than in Nissum Bredning. At certain times the plaice in Nissum Bredning mainly contained *Macoma baltica* (April), *Nucula* (May), *Abra alba* and *nitida* (August) and *Philine* (October); but both *Solen* and *Mya* are seldom there and these two with *Abra* are certainly the choicest Lamellibranchs of the plaice in the Limfjord; that the quantity of *Abra* does not increase here more than from 0.23—3.0 gm. must certainly be ascribed to the enormous amount it is sought after. The increase of *Nucula* in the autumn is perhaps due to the fact, that the plaice does not seem to be specially fond of this Lamellibranch, which is evidently »heavy on the stomach«, often closed and unbroken. In the spring however many are devoured in Nissum Bredning. It seems therefore, that the quantities of dry matter, ca. 30 gm. per 10 m.<sup>2</sup>, the eel and plaice digest in Thisted Bredning, do not mean much by comparison with the great production of up towards 200 gm. per 10 m.<sup>2</sup> of the lower animals here; but there is a great difficulty just in this Bredning in determining, what quantities of animals are at the disposal of the fishes, this namely, that only a portion of the quantities of *Mya truncata* is eaten by them; some are too large for them to swallow. To determine which are small enough to serve as fish-food, is not easy, as it seems that both the eel and the plaice can bite off the siphons of the larger *Mya* and thus obtain a portion of the larger animals. As the quantity of *Mya* is so greatly in excess of all others, this fact leaves a big margin in the determination of the available quantity of fish-food. Many *Mya* are eaten, especially the smaller at any rate of up to 2—3 cm. length of shell; this Mollusc is at times extremely common in the stomachs of plaice both in Thisted Bredning and at several other places in the Limfjord (Livø Bredning several places, Risgaard, Hvalpsund and Skive); but not in Salling-sund, Kaas and the western reaches, where large *Mya* is to be considered as a

great rarity, at least in these years. I have been much astonished to see, how the young *Mya* have decreased in numbers in Thisted from 1909 to 1910 (see Table V), but the numbers of the adults increased in the same time. Can this be the result of the great transplantation of plaice which began in 1908? If so, then *Mya* will eventually die out here, perhaps the process is going on now; possibly it is just the persecution of the young individuals by the plaice, which has led to scarcity of *Mya* in the western reaches and Sallingsund; here there is always a large and abundant stock of plaice. It will be of interest to follow the further development of this matter in subsequent years; *Mya* will possibly become rare in Thisted, as it is now in Kaas and Sallingsund, and other Lamellibranchs such as *Solen* and *Abra* will take its place, which they seem to be able to do on account of their numbers and rapid growth; the annual production of plaice on these 2 last-mentioned areas is namely much greater per m.<sup>2</sup> than on the areas where plaice are implanted; the plaice it is true do not grow so rapidly here as in Thisted, but the stock of them is much denser.

Whilst therefore we can make an endeavour to determine approximately the consumption of food by fishes at several places in the Limfjord, we are quite helpless, as said, in regard to the determination of the consumption of the whelks and starfish; in consideration of the great mass of these animals this consumption must probably be great, perhaps greater than that of the fishes; their total mass of dry matter was indeed ca. 5 times larger than that of the latter. If we place the consumption of these animals at twice that of the fishes, thus ca. 60 gm. per 10 m.<sup>2</sup> we obtain

Consumption of the fishes.....	ca. 30 gm. dry matter per 10 m. <sup>2</sup>
Consumption of whelks and <i>Asterias</i> ..	ca. 60 - - - - -

What is further produced as increase in the course of the year, including here the increment for *Mya*, ca. 200 gm. dry matter per 10 m.<sup>2</sup>, must be added as provisional excess, in order to obtain the total production of dry matter per m.<sup>2</sup> This would be therefore, at the lowest estimate, about 300 gm. or 30 gm. per m.<sup>2</sup> In Thisted Bredning the total quantity of the dry matter of the bottom-fauna per m.<sup>2</sup> was somewhat similar.

The fauna living on the bottom would thus as a whole reproduce its own mass each year; some species are known to do this several times over (*Abra*), others probably cannot do so; the main result seems therefore not improbable.

I do not lay exceedingly great weight, as mentioned, on these preliminary results; but in order to carry the principle of metabolism as far as possible, we must also endeavour to understand, on what materials and what quantities this bottom-fauna is nourished. The dry matter of the bottom-fauna per m.<sup>2</sup> was ca. 30 gm.; if we reflect now on its comparatively rapid growth, we may well assume that, like the fishes, it consumes its own weight several times yearly; it must therefore use up a quantity of organic matter which is several times larger; and we must remember here that the shells of the large animals and the chalk of the Echinoderms are not included in the quantity of dry matter. This quantity of food is obtained by the bottom-animals, as already mentioned, mainly from the everywhere present, dust-fine detritus, the origin of which is due in the first place to the bottom-flora. No measure can yet be given of the annual production of

this flora, but it is enormously great in the Limfjord. Nor have we any measure of the plankton production in the Limfjord; but to judge from my plankton investigations in 1898—01 (Vid. Selsk. Skrifter 6. R. XII. 3. 1903 pp. 18—19), the volumes do not seem in any way so great in the Limfjord as at Lyø in the western Baltic. The shallow water of the Limfjord does not give so much room for plankton development as the much deeper western Baltic; for the latter we have from Hensen in his first great plankton work a preliminary endeavour to determine the annual production of the plankton per m.<sup>2</sup> in gm. of organic dry matter. He finds, that in addition to the quantity of plant plankton which is consumed by the plankton animals, there is produced here 14—16 gm. organic dry matter per m.<sup>2</sup> annually. This is obviously but a small quantity, even in this water, in comparison with the quantities of dry matter, which must be used by the bottom-fauna in the less plankton-rich waters of the Limfjord. I have already suggested (Report VII 1897 p. 23), that the quantity of the plankton in the Limfjord might perhaps have an appreciable influence on the food of the fish-stock from one year to another; I must now give up this idea; we must study the richer sources for the production of matter, to be able to find any such influence.

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## XI. Conclusion.

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What we specially require to do in the future to round off these investigations, in addition to making more enumerations at different times of the year and studying the relation between producers and consumers as well as the weight of the animals, is to bring the plant belt under quantitative treatment, both in regard to the determination of the mass of the animals living there and the mass of the bottom-flora per m.<sup>2</sup> With the aid of a suitable motor-boat, I believe that this could be done.

There remains also to obtain the best possible insight into the mass and food-consumption of the necton, especially of the fishes. It will only be when our knowledge both of the benthos and necton has advanced in the direction of quantitative determination, that we shall be able to estimate the importance of the plankton. By plankton I mean here living plankton organisms and what comes therefrom. The mass of their producers seems however, both from Lohmann's investigations and from Hensen's older work in the western Baltic, not to be of great importance for the benthos animals, as we must conclude, that they do not even satisfy, at any rate at certain times of the year, what the consumers of the plankton itself require for food; Lohmann refers therefore, to the dust-fine detritus in the sea as further source of food for the plankton animals; in the Limfjord this detritus is certainly in the main of benthos origin.

We might perhaps sketch out the main lines of the conditions as follows;

the consumers of the plankton rely essentially upon the producers of the plankton; in the neighbourhood of the coasts the detritus of the benthos also contributes to increase the mass of the plankton animals, which here like that of the benthos fauna is large; in the open seas where the quantity of the benthos detritus is small, the plankton has only its own producers to rely upon; its mass is therefore smaller and there is only a very sparse benthos fauna here; »the region of the very deep sea far from land may be called deserts when compared with the teeming life of the surface and shore waters«, writes John Murray in 1910 after his last expedition in the Atlantic with Johan Hjort onboard the »Michael Sars«. Whatever the conditions may be, I am of the opinion there can be no doubt, that in the Limfjord the food of the fishes (eel, cod and plaice) is obtained in greatly preponderating degree from the benthos fauna; this is represented in Table V. The food of this benthos fauna is the dust-fine detritus which again arises in the main from the benthos flora, namely *Zostera* and marine algae large and small. It is thus this flora which is the basis of the fish-life in the Limfjord and certainly in many other coastal waters. In the specially plant-rich and enclosed parts of the Limfjord this flora is probably too abundant to offer suitable conditions of nourishment for the small animals of the benthos fauna; at other places in more open parts it is perhaps too scarce to produce the maximum animal dry matter per m.<sup>2</sup> This leads naturally to the suggestion, that in future the vegetation might also come under suitable treatment, such as removal from some places, transference to others, for example by cutting down, just as is done in the case of other plants in freshwater cultures, dredging, collection of seaweed or perhaps by intensive eel-spearing in the plant belt; a large production of the food-animals of the bottom-fauna (worms, Molluscs etc.) is obviously the first condition for a rich production of eel and plaice. Of these we can get a sufficient quantity of the young; the limit of production of eels and plaice is clearly set by the available amount of fish-food.

As is known, the Limfjord was the first expanse of salt water, where the endeavour was made to eke out the stock of plaice by transplanting fish from overcrowded places to places with greater possibilities of growth; a method which had long been known in the case of the freshwater fisheries. The possibility of combating the harmful animals has for long claimed attention in the Limfjord; artificial hatching of these fishes is superfluous, though perhaps the rearing of lobsters and prawns is a different matter; legislation has been in force in the Limfjord for hundreds of years; the only thing remaining therefore is treatment of the bottom, so that its economical management may on the main principles be raised to the level of that of the freshwaters, and the present investigations seem to offer many possibilities for such treatment. In the case of the freshwaters, as is known, bottom-treatment of various kinds plays a very great role.

It is our hope that these investigations of ours will lead to a series of similar investigations in other lands; we believe that our methods and apparatus, at least in a form suited to the various conditions, will fill a more or less consciously felt want with many who are engaged in the study of the metabolism of the sea.

We have not yet made investigations in the dense part of the plant belts, it is true, but with a change in the 0.1 m.<sup>2</sup> bottom-sampler it is certain that such

will be able to be carried out. In the deeper parts of the freshwaters, where the deposits are usually soft and the depths small, lighter bottom-samplers can certainly be used from small boats; if it is desired to use larger bottom-samplers from large ships such can probably be constructed quite easily. In the larger seas it is obvious that it would be an advantage to use large bottom-samplers, as at many places not many organisms will come into these; the reason why we ourselves have not felt it necessary to use larger is, that the small (0.1 m.<sup>2</sup>) are well suited for our fjords with their large number of small animals.

We have here a new field of work, which is very large and seems promising. Enumeration of the bottom-animals does not take up so much time as counting of the plankton; and when the percentage of dry matter has been determined for the different years, the number of individuals, as also the total rough weight of the species per 100 stations or fewer, will give good information regarding the mass of the animal life per m.<sup>2</sup>

I am inclined to believe, that an evaluation with such bottom-samplers could be carried out comparatively easily, and would lead much further than plankton determinations alone can, in the direction of the determination of the mass of fish food. We may certainly with Hensen consider it a *conditio sine qua non*, that we must know on the main points the capacity of a water as regards the production of fish-nourishment, in order to be able to judge as to its rational exploitation in the interest of the fisheries. It will however scarcely be an easy matter to determine exactly, by quantitative investigation of the food-animals alone, the quantity of food available yearly, annual food-production, for the consumption of the fishes or other animals in any water; nor is it practically possible in the case of the plankton; it is only the logical consequence of our scientific mode of working to attempt to do such a thing. Both Hensen and the present work endeavour therefore at the same time to find another, more direct way, namely, to determine the production of food by investigating, what is actually used of the food by fishes or other animals which have lived on this food. When we have determined in this way, how much a sea-bottom can produce, **it is comparatively easy by means of the bottom-sampler to compare this bottom with another** and thus obtain a good insight into, whether the one or the other is best suited for the production of the one or the other kind of food-animals, this or that species of fish, and whether on the whole it is more productive than the other. It is this I have in mind in using the expression "**valuation of the bottom**". The importance of such a valuation in the comparison of areas on land and in the whole practice of agriculture is well known; it is time we introduced similar methods in sea-culture. In the case of freshwater areas, one or several methods of valuation have been experimented with (Walter, Zuntz), with more or less success; that several important freshwater fishes take vegetable food as well as animal, complicates the conditions here a good deal; further the principal food-animals in freshwater (Crustacea) seem to be very small and not specially bound to the bottom; enumeration and bottom-sampling are thus made difficult; it is much easier to count the plaice-food in the Limfjord. Perhaps the proper apparatus have not yet been found. I should be inclined to think, that suitable, modified forms of the

0.1 m.<sup>2</sup> bottom-samplers would prove to be practical here. In Denmark the fresh-water and saltwater are so closely connected, that this matter is of importance for both; the large dams we have constructed, for example at Salbæk-Vig, have in part been based on the German principles of carp culture, as the result of investigations made by Germans called in for the purpose; it is time that such undertakings should be studied also from the Danish side; as the results hitherto have not been specially good. An evaluation will probably be able to show, whether they can be carried out better, and will possibly throw light on whether quite other methods should not perhaps be introduced. At the present time all the organic material of the surrounding land is usually conducted out to the sea by means of canals, without being of any use to the ponds, and perhaps also without being of use to the sea.

Naturally the evaluation will give results most quickly in the case of the small waters; but even in the large seas we must sooner or later come to it. In the sea the determination of the mass and production of the bottom-plants is made much easier by the fact, that they only grow in shallower water, as also that they are probably not eaten up, whilst living, by the animals as a rule; for an extremely large number of algae we might therefore take almost the whole of their maximum quantity present as the annual production, as many are annuals; in the case of the *Zostera* and similar plants, it will probably be easy to ascertain, by closer study of their growth, how much they produce annually. At the places where the bottom is covered with stones, or formed of rocks, determinations with the bottom-sampler may perhaps be impossible; but here as a rule it is possible to carry on diving operations.

No large open water has been better and oftener investigated probably than the North Sea, its coasts in the south and east perhaps most of all; but these are so little covered with vegetation, that we involuntarily, on a long acquaintance with them; obtain the impression; that the bottom-vegetation on the open coasts is on the whole of very little importance; this however is not the case; journey over to the rocky coasts of England and Scotland, to Norway with its cliffs and reefs and fjords, at places very broad and still unmeasured and numerous, not to say innumerable; there we find vegetation which is of some importance; and all the sheltered fjords have their superfluity of algae and *Zostera*; nor do they keep these to themselves, but scatter them far and wide in the sea, as Boysen Jensen points out. And consider the quantities carried down into the North Sea by the large rivers of Middle Europe and England!

What is the origin of the rich mud-lands (marshes) of Holland, Friesland, Holstein and Sleswig? Until we have found our way in these questions, and have learnt to use measures and weight, as Hensen has taught us for the plankton, we shall never rightly understand, what forms the basis of the great fish-wealth of the North Sea and its coastal waters or what we can expect to get from them.

After I had learnt, what the fine detritus of the bottom and the water means for the lower animals, I endeavoured to fix up a small aquarium with water and bottom-soil of detritus from the Great Belt, the same mass of water being used always, never filtered and only air drawn through it. It appears, that *Asterias*, *Ophioglypha albida* and *Buccinum*, *Fusus*, *Littorina littorea*, *Abra*

*alba*, *Mytilus edulis*, *Solen*, *Astarte borealis*, *Cynthia*, *Idothea marina*, *Gammaridae* etc. thrive excellently in it. For about 3 months the water has kept clear in a cool room. »Plankton« apart from bacteria is not present in the water; but the animals live well and *Abra* has grown considerably in the interval. The aquarium is 45 cm. long, 18 cm. broad and 31 cm. high. I have already made many new observations of great interest in this little aquarium, some of which have been already mentioned; and I expect that aquaria populated in the right way, will give much information regarding many of the questions, it is not possible to solve in open nature, and am inclined to believe, that through such aquaria we may find a way to make many experimental investigations on the animal life of the sea, especially in biological regards. One may wonder also, whether the large, public aquaria could not try to approach nearer to the natural conditions on the sea-bottom, so that the animals could find suitable conditions of nourishment in them; many of quite the commonest marine animals are never seen in such aquaria, simply because they will not thrive without the bottom-detritus. A certain amount of courage is required to place the dark, dust-fine mud from the sea-bottom in an aquarium; the whole water comes to look like undiluted mud; but after a time a change occurs, the water clears and the animals become satisfied with their surroundings. We must naturally take care, that there is a proper proportion between the bottom-materials, quantity of animals, quantity of plants and amount of water, but it is only by experiment that we can ascertain the right proportions. A suitable temperature is naturally also a necessity.

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### Résumé.

After Petersen's earlier investigations on the oyster and other bottom-animals of the Limfjord had shown, what a slight importance in quantitative regards the plankton had for the nourishment of these animals, he began with Boysen Jensen a study of the dust-fine mass which usually forms the principal contents of the stomachs of the bottom-animals, which are not predatory or plant-feeders.

The dust-fine mass is partly of inorganic, partly of organic origin, but quantitatively seen living organisms are seldom contained in it. A study of the bottom-flora shows its extent and distribution in the Limfjord and how little comparatively it is used in the living condition as food for animals; on the other hand, a close connection is shown between the density of this flora and the amount of organic matter contained in the sea bottom, from the North Sea to the Baltic. The enclosed fjords are richest both in bottom-vegetation and organic material in the deposits of the sea-bottom; the quantity of the plankton here does not seem to have any recognizable influence. By means of bottom-samplers and glass-tubes it is shown, that the uppermost brown layer of the sea-bottom (ca.

2—3 mm. thick) must be regarded as dust-fine detritus containing remains of almost all durable parts of organisms, but in the main its organic content is certainly formed of deposited, dust-fine or larger parts of the plants from the benthos vegetation. Whilst the contents of this brown layer and its degree of oxidation make it specially well-suited as nourishment for the animal life of the sea bottom, the underlying layers are of quite a different nature. There is no recognizable difference between the stomach contents of the Molluscs and the components of this uppermost brown layer.

Centrifuging of Limfjord water shows quantities of dust-fine detritus in this of quite similar nature to that in the brown layer of the bottom. The quantity of the plankton organisms is inappreciable in comparison with the quantity of the dust-fine detritus. In several enclosed fjords with rich bottom-vegetation large quantities of dissolved organic matter have been found in the sea-water.

The deposited detritus and its quantity have been studied by means of tubes (detritus-collectors) specially set out on the bottom; the quantity proved to be very dependent on the strength of the wind, as the motion of the waves in the shallow Limfjord, as a rule only 8—12 meters deep, can obviously stir up the fine soil of the bottom.

A study of the literature shows, that at other places both in Europe and America similar contents have been found in the digestive canals of the oyster and other animals, but there has always been some hesitation in believing, that anything from the dead material of the sea-bottom could be of importance as food, partly because only the black, underlying mass of mud has usually been noticed when brought up by the dredge and thus the uppermost, thin brown layer has escaped attention, partly because one cannot directly see any difference in the detritus before and after it has passed through the gut of the animals. The American investigations on the quantity of living organisms in the gut of the oyster have shown, however, that this is so small, ca.  $\frac{1}{8}$  mm.<sup>3</sup>, that in our opinion it cannot possibly constitute the food of the oyster.

In recent years, however, Lohmann for the plankton animals and Rauschenplat for the bottom-animals have taken some notice of the detritus as food.

To study the food of the bottom-animals we selected the whole of a restricted animal community in one of the most enclosed parts of the Limfjord (Thisted Bredning); here it appears that by far the majority of the animals are detritus-feeders and obtain the detritus partly from the water partly from the uppermost brown layer on the bottom, the origin of which is mainly of a benthonic nature. The plants of the plankton must rather be considered as serving as food for the plankton animals, but they are not always sufficient for this (Lohmann). The benthos vegetation must therefore be ascribed a very great importance as source of food, among others, for the benthos animals in the Limfjord. It is mentioned, that both Hensen and later K. Brandt have been aware that the plankton cannot alone supply food for all the animal life of the water, and it may be considered, that only the lack of methods for the quantitative study of the benthos has prevented them from also making such experiments. To



measure the quantity of the organisms in the sea, which forms the basis of our investigations, is therefore only a logical continuation of the principle of Hensen. After many years' work in this field, Petersen has succeeded in constructing a suitable apparatus (bottom-sampler 0.1 m.<sup>2</sup>) for making quantitative determinations of the mass and number of the bottom-animals per square unit of area. Investigations with the apparatus as figured here have been made at many places in Danish waters from the North Sea to the Baltic, and tables are given here, based as a rule on 50—100 samples with the bottom-sampler, showing the species, number, rough weight and amount of dry matter for the bottom-animals. The last factor gives the best measure for the mass of the organic matter in the bottom-fauna per m.<sup>2</sup>; in the case of the Molluscs and Echinoderms the calcareous matter is not included in the amount of dry matter. Information is given regarding the quality and quantity of the bottom-fauna at several places in Danish waters; both vary greatly from one water to another, and the fauna is obviously of very different productive capacity. At one place the large, old, strongly calcified animals with very small percentage of dry matter are predominant; here the production of organic matter is obviously but small; the quality is bad. At other places, especially in the fjords, we find small, rapidly growing animals in large numbers; here the production is certainly large; the quality is good. In the Limfjord (Thisted Bredning) the endeavour is being made to carry these investigations a step further forward, partly by examining a large number of stations several times in the year, so as to obtain more light on the extent of the increase in growth or increment, partly by determining the consumption through a study of the amount annually used by fishes and predatory animals (whelks, *Asterias*). Here the fisheries statistics give good information, and the daily consumption of food by the plaice is being determined by investigations in nature; each day it digests at least the whole contents of its digestive canal. The consumption of the fishes seems but little by comparison with the total amount of dry matter available; the quantity of the whelks on the other hand is greater than that of the fishes. Taking everything into account we may conclude, that the bottom-fauna as a whole annually renews its own mass, and that in the Limfjord therefore it cannot possibly be satisfied with the amount of food, the plankton according to Hensen's, certainly provisional, determinations can offer.

Although we cannot attach too much weight to the figures gained by these investigations, owing especially to the various shortcomings — the bottom-sampler cannot be used everywhere, e. g. not on stony ground, the investigations are not sufficiently numerous, various side-questions not sufficiently studied etc. — we ascribe great importance to the whole sequence of ideas which forms their basis, and especially to the idea, that the benthos organisms must also be investigated quantitatively, so that we may be able to form a true picture of the metabolism of the sea. We believe, that such investigations would very quickly lead to complete and useful results in the smaller, enclosed waters; but we are also of the opinion, that quantitative determinations of the animal life of the sea-bottom in the open waters will become necessary sooner or later, if we are ever at all to form any conception of the

productive capacity; -- larger bottom-samplers suited to this purpose can easily be constructed probably, with the one described here as pattern; only with the aid of such, specially suited apparatus are quantitative investigations possible. The dredge cannot be used.

We have reason to believe, that certain, enclosed parts of fjords in Denmark contain such a rich vegetation, that the bottom is less suited to hold a richly producing bottom-fauna; and we can thus imagine the possibility of being able to improve the bottom-conditions by cutting down a portion of the superfluous vegetation by means of sailing or steaming reaping machines. Such indeed have already been used in the large European freshwaters, where the vegetation has become too troublesome. We mention this here as an example of the fact, that an exact knowledge of the quantity of organisms at the different places, in addition to the mutual relations of the organisms, is necessary before we can venture to interfere in a right way in the workings of nature, and before we can judge of the consequences of the interference which is made already by man to such a great extent, especially in our smaller and very restricted, but obviously very productive fjords and small waters.

So far as it lies in our power, our investigations will be continued and extended, so that they may be able to yield as accurate results as possible.

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## Explanation of the Plates.

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Plate I. Fig. 1: The earlier bottom-sampler on pole. Figs. 2 and 3: A recent model of the  $0.1 \text{ m.}^2$  bottom sampler; open (2) and closed (3). All the figures much reduced.

— II. The commonest animals on the soft bottom in Thisted Bredning. All figures in the natural size.

Fig. 1. *Trochus cinerarius*.  
› 2. *Nassa pygmaea*.  
› 3. › *reticulata*.  
› 4. *Buccinum undatum*.  
› 5. *Littorina littorea*.  
› 6. *Acera bullata*.  
› 7. *Philina aperta*.  
› 8. *Abra alba*.  
› 9. *Cardium fasciatum*.  
› 10. *Macoma baltica*.  
› 11. *Nucula nitida*.  
› 12. *Solen pellucidus*.  
› 13. *Corbula gibba*.  
› 14. *Mytilus edulis*.

Fig. 15. *Cyprina islandica*.  
› 16. *Mya truncata*.  
› 16ab. › › The sizes eaten  
by plaice.  
› 17. *Aphrodite aculeata*.  
› 18. *Nephtys coeca*.  
› 19. *Pectinaria belgica*.  
› 20. Gammaridae.  
› 21. *Diastylis Rathkii*.  
› 22. *Idothea*.  
› 23. *Ophioglypha texturata*.  
› 24. *Asterias rubens*.  
› 25. *Echinocyamus angulosus*.  
› 26. *Echinus miliaris*.

— III.  $0.25 \text{ m.}^2$  of sea-bottom in Thisted Bredning with its average fauna. Natural size.  $19/10$  1910. (see Table V).

— IV.  $0.25 \text{ m.}^2$  of sea-bottom in the Kattegat, west of Høganæs.  $19/7$  1910. (see Table VI).

— V.  $0.25 \text{ m.}^2$  of sea-bottom in Holbæk Fjord and Bramsnæs Vig.  $6/5$  1910. (see Table VI).

— VI.  $0.25 \text{ m.}^2$  of sea-bottom in the Baltic. E. S. E. of Høje Møen.  $25/7$  1910. (see Table VI).

The Plates III—VI have been drawn schematically to represent the density of the population on the sea-bottom; each represents  $50 \times 50 \text{ cm.} = 0.25 \text{ m.}^2$  of sea-bottom, natural size, with the average fauna belonging thereto in natural size. On such a small space of sea-bottom it is impossible to reproduce exactly the mass of the fauna; often only a portion of an individual of a species should be represented; to counterbalance this I have sometimes combined nearly related forms to one individual, or have represented a small individual, so as to come as near as possible to the portions found; these difficulties naturally occur most often in the case of the least frequent species. Reference may further be made to the text, especially the section on: The mass and composition of the bottom-fauna at several places in Danish waters.

It would be of interest from a biological standpoint to have such quantitative pictures made of a large area of the sea-bottom; this is not possible in natural size on Plates; it might be done in biological museums.

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## Information

regarding the XVIII places mentioned in Table VI and on the Charts II and III, with respect to position, depth, bottom, vegetation etc.

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- No. I. S. W. of Hals Lightship, 6. September. 10 stations and 5 samples at each. Depth 7—8 meters. Sandy bottom with green *Zostera*, *Furcellaria* and *Halidrys*. 5 samples in each sifting.
- No. II. S. E. by E.  $\frac{1}{2}$  E., 15 miles from Muldbjærgene, 6. September. 10 stations and 5 samples at each. Depth 10—11 meters. The bottom consists of fine sand without vegetation. 5 samples in each sifting.
- No. III. W. N. W. and 9 miles from Kullen, 18. July. 10 stations and 5 samples at each. Depth 30—34 meters. The bottom consists of fine gray clay with large quantities of empty Gammarid tubes which made the sifting difficult. 1 sample in each sifting.
- No. IV. The Sound, »Sandet« off Snekkersten, July 20. 5 stations and 10 samples at each. Depth 3—4 meters. The bottom consists of pure white sand without vegetation. 10 samples in each sifting.
- No. V. The Sound, »Lous Flak«, 20.—21. July. 10 stations and 5 samples at each. Depth 9—11 meters. The bottom consists of soft, black, stinking sand with a little, perhaps loose *Zostera*. 5 samples in each sifting.
- Nr. VI. The Sound. S. W. of Hven, 21. July. 10 stations and 5 samples at each. Depth 14—16 meters. The bottom consist of sand with gray detritus. 5 samples in each sifting.
- No. VII. The Sound. N. of Hven, 21. July. 10 stations and 5 samples at each. Depth 21—31 meters. At the first 5 stations the bottom consists of black masses of detritus, and at the last 5 stations of more grayish material, but softer than elsewhere in the Sound. 5 samples in each sifting for the first 5 stations, 2 to 3 samples in each sifting for the last 5 stations.
- No. VIII. W. of Høganæs, 4 miles, 19. July. 10 stations and 5 samples at each. Depth 20—24 meters. The bottom consists of gray clay with some sand. 5 samples in each sifting.
- No. IX. Great Belt, S. S. E. of Sprogø, 1. August. 10 stations and 5 samples at each. Depth 20—26 meters. The bottom consists of fine sand with a little, brownish gray detritus, at the last 3 stations mixed with small stones. 5 samples in each sifting.
- No. X. Samsø Belt, W. of Ringebjærg, 4 miles, 5. August. 1 station with 10 samples. Depth 14 meters. The bottom consists of coarse sand mixed with a little clay. 3 samples in each sifting.
- No. XI. Samsø Belt, W. of Ringebjærg, 2 miles, 5. August. 1 station with 10 samples. Depth 21—36 meters. The bottom consists of coarse sand with a little clay, and small stones in the last samples. 2 samples in each sifting.

- No. XII. S. E. of Stevns Light, ca. 10 miles, 25. July. 10 stations and 5 samples at each. Depth 23—25 meters. At the first 4 stations the bottom consists of fine sand and at the last 6 stations of coarse sand. 5 samples in each sifting. Many young *Mytilus edulis* were found at this place.
- No. XIII. E. S. E. of Høje Moen, ca. 15 miles, 25. July. 10 stations and 5 samples at each. Depth 35—42 meters. At the first 3 stations the bottom consists of sand and at the last 7 stations of gray detritus. 5 samples in each sifting.
- No. XIV. North Sea, W. of Agger, ca. 4 miles, 7. July. 1 station with 10 samples. Depth 20 meters. 5 samples in each sifting.
- No. XV. Roskilde Fjord, open part, 9. May. 5 stations and 1 sample at each. Depth 4—5 meters. The bottom consists of quivering, black, stinking detritus with a brown, uppermost layer ca. 10 mm. thick.
- No. XVI. Kulhusrenden, Frederikssund, 7. May. 10 stations and 1 sample at each. Depth  $3\frac{1}{2}$ —12 meters. Variable bottom-soil, sand, gravel, detritus and dead *Zostera*.
- No. XVII. Holbækfjord and Braamsnæsvig, 6. May. 15 stations with 1 sample at each. Depth 3—8 meters. Usually black quivering mass of detritus with *Zostera*.
- No. XVIII. Isefjord, open part, 6. May. 10 stations with 1 sample at each. Depth 9— $10\frac{1}{2}$  meters. The bottom sandy, with quivering detritus mass.







Fig. 2.

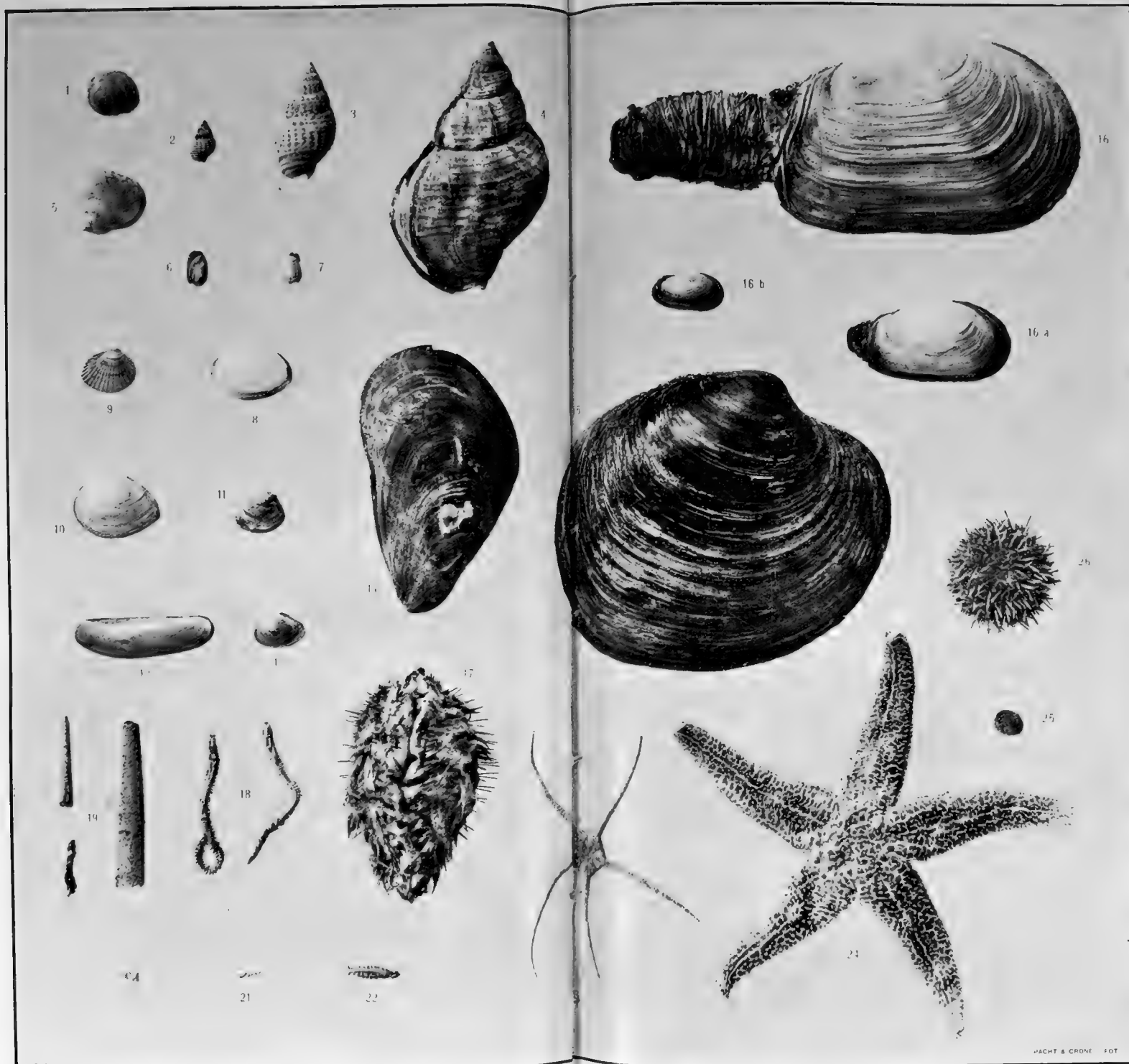


Fig. 1. Earlier apparatus with pole, to take up 1 square foot of bottom-soil.



Fig. 3.









# L I M F J O R D E N .

Chart No. 1.



Centraltrykkeriet

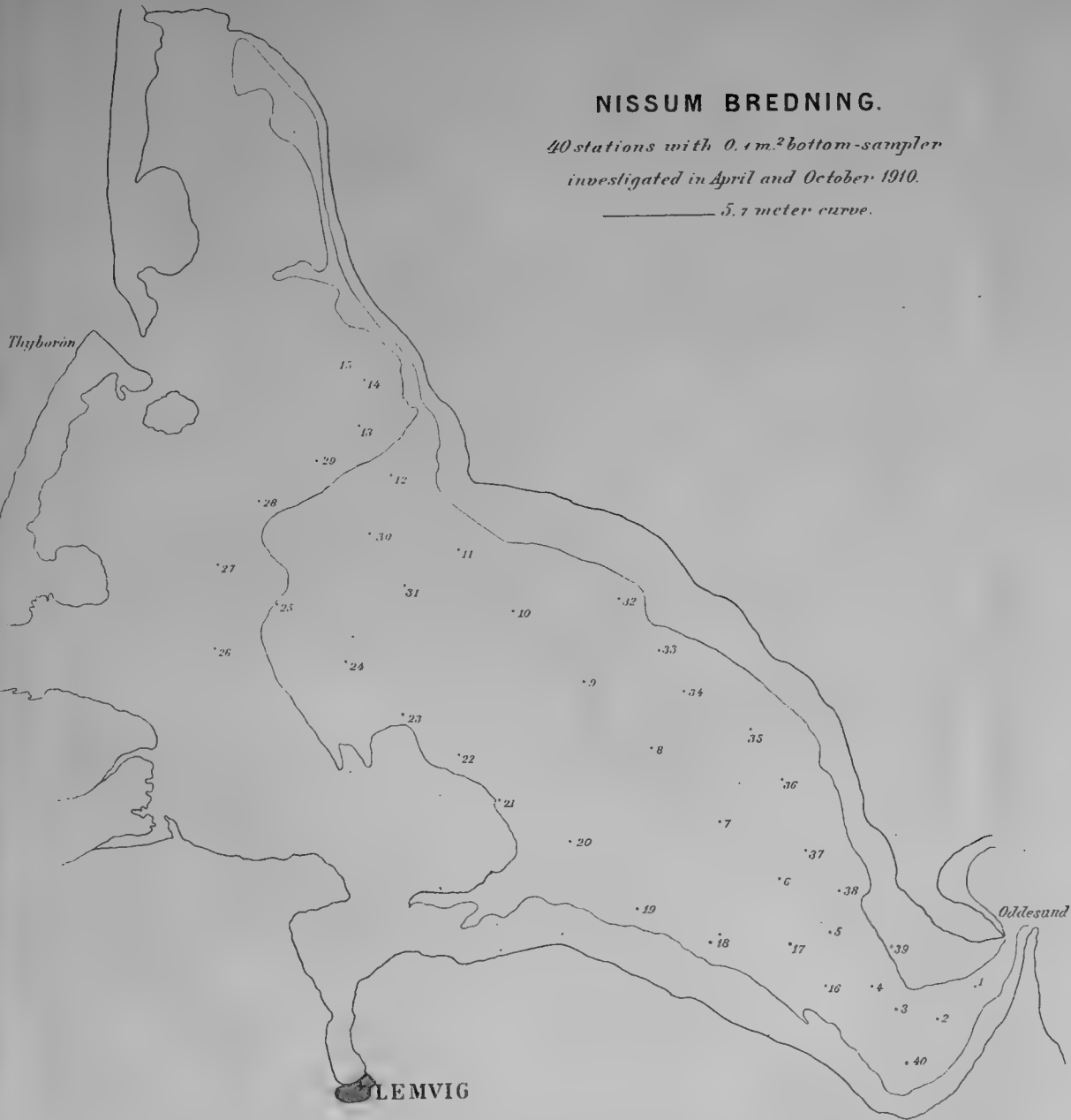


The shading indicates the Zostera-region.

### NISSUM BREDNING.

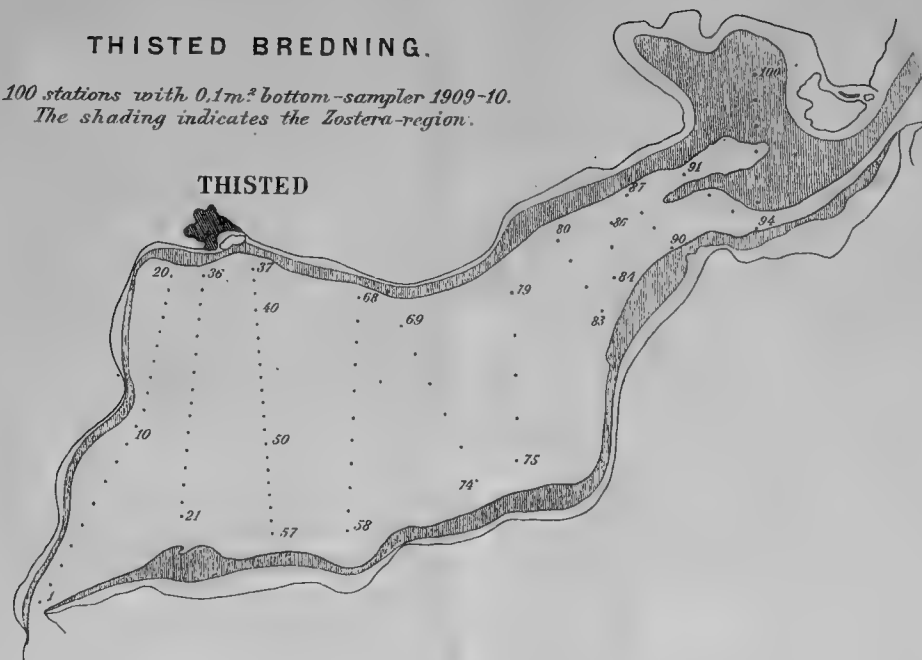
40 stations with 0.1 m.<sup>2</sup> bottom-sampler  
investigated in April and October 1910.

————— 5.7 meter curve.



### THISTED BREDNING.

100 stations with 0.1 m.<sup>2</sup> bottom-sampler 1909-10.  
The shading indicates the *Zostera*-region.

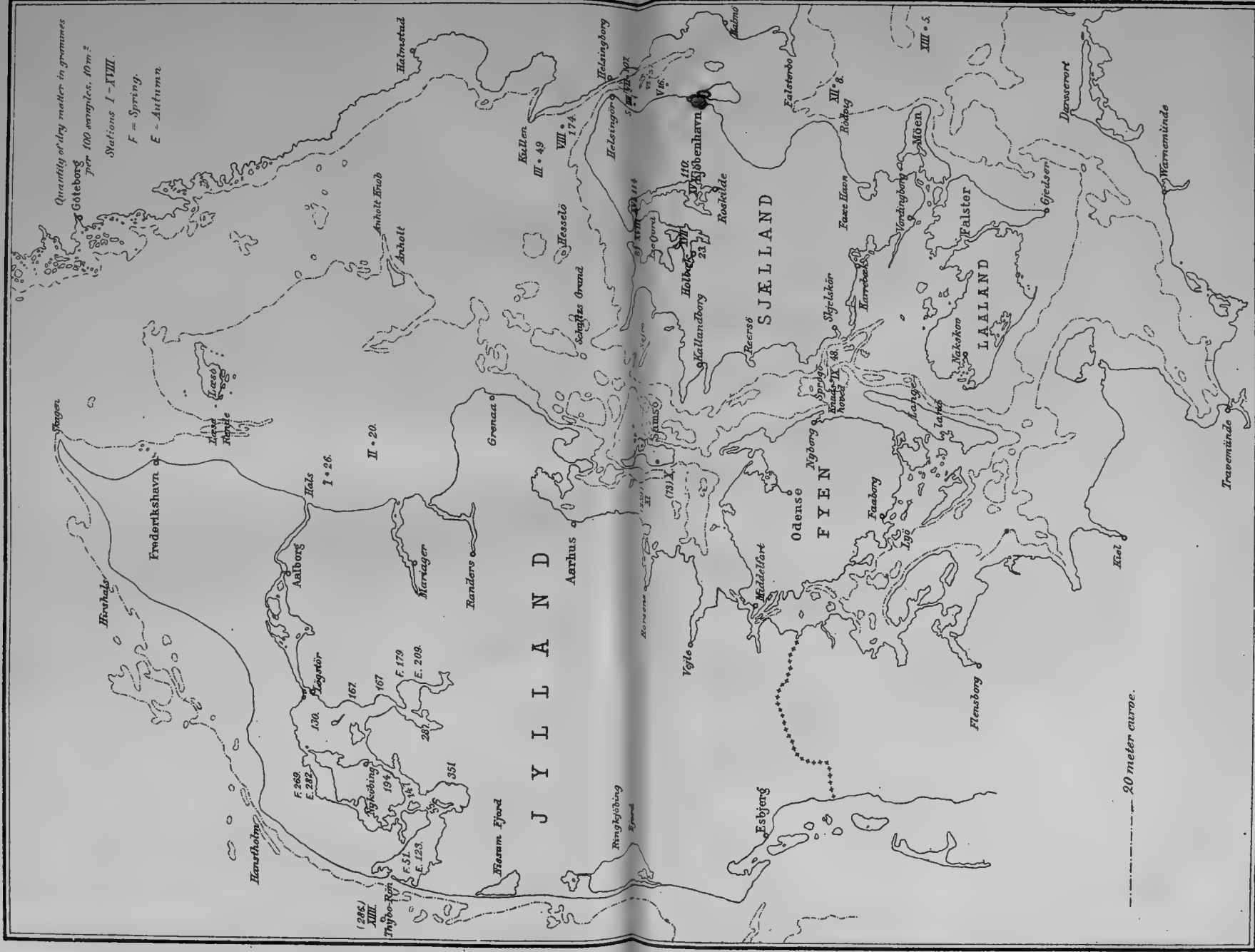












































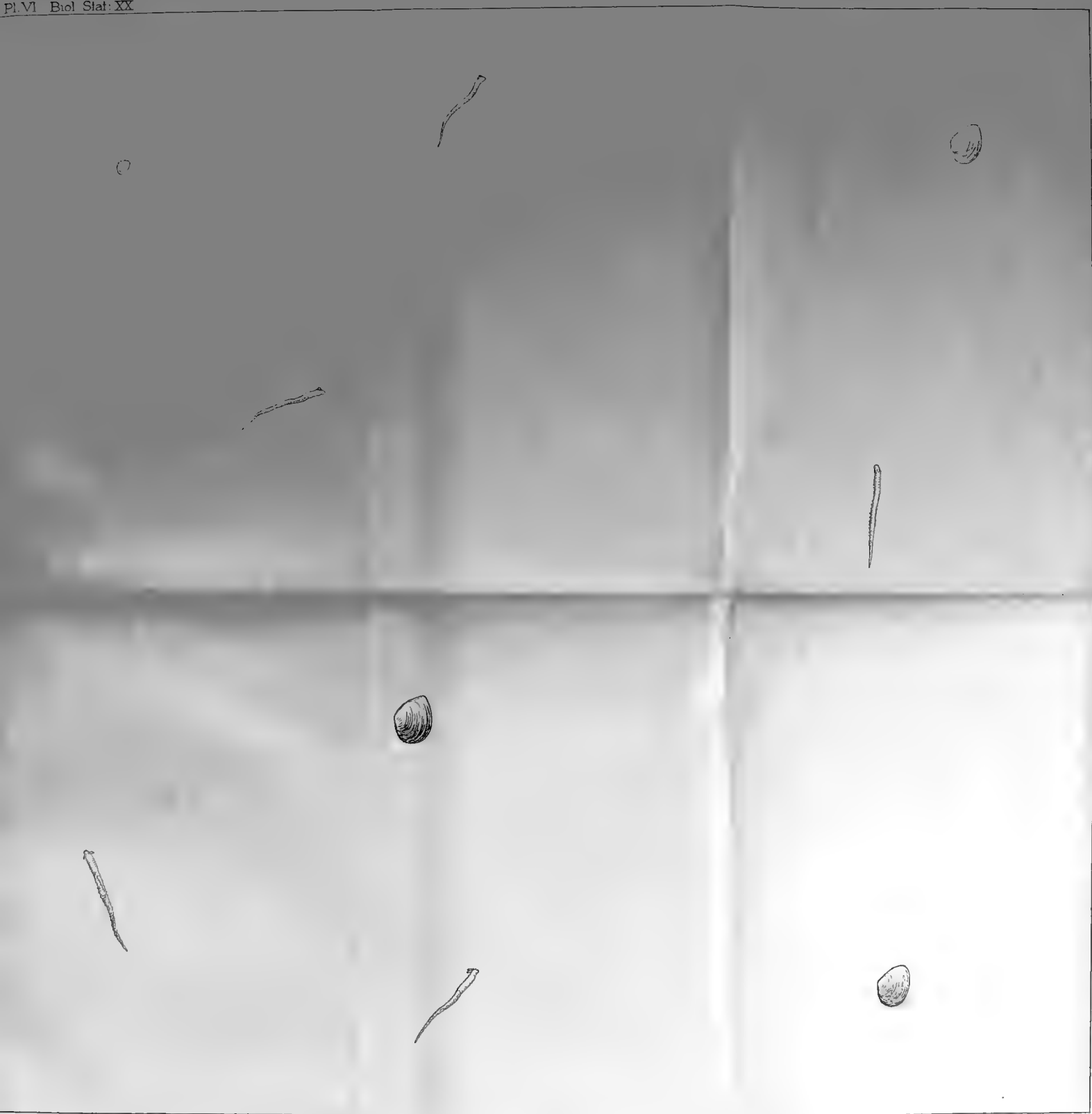
















C. G. Joh. Petersen: Om de skalbærende Molluskers Udbredningsforhold i de danske Have indenfor Skagen 1888. 8°. 1162 pg. 2 Kort.

Det videnskabelige Udbytte af Kanonbaaden »Hauch«s Togter i de danske Have indenfor Skagen. 1893. 4°. 464 pg. Atlas i folio.

Indhold: Echinodermata (Petersen), Diatomæer (Cleve), Undersøgelse af nogle Bundprøver (Rørdam), Mollusca (Petersen), Cephalopoda (Posselt), Crustacea malacostraca (Meinert), Hydrografi (Rørdam), Polyzoa (Levinsen), Ascidiæ simplices (Traustedt), Annulata, Hydroidæ, Anthozoa, Porifera (Levinsen), Nogle alm. Resultater (General Results. Engl.) (Petersen).

C. F. Drechsel: Oversigt over vore Saltvandsfiskerier med Kort og Planer. 1890. 4°, 100 pg. Med et Tillæg: »Om Naturforholdene indenfor Skagen« af C. G. Joh. Petersen. Med Kort. 4°. 46 pg.

Fiskeri-Beretning for 1888—89, 89—90, 90—91, 91—92, 92—93, 93—94, 94—95, 95—96, 96—97, 97—98, 98—99, 99—1900, 1900—01, 1901—02, 1902—03, 1903—04, 1904—05, 1905—06, 1906—07, 1907—08. 1908. 1909.

Beretninger fra den danske biologiske Station findes paa dansk publicerede i de tilsvarende Fiskeri-Beretninger.

- I. Fiskenes biologiske Forhold i Holbæk Fjord. 1890—91. 63 pg. Med et Kort.
- II. Om vore Kutlingers (*Gobius*) Æg og Ynglemaade. 1892. 9 pg. Med 2 Tavler.
- II. On the Eggs and Breeding of our Gobiidæ. 1892. 9 pg. Two Plates.
- III. Det pelagiske Liv i Fænø Sund etc. 1893. 38 pg. Tabeller.
- III. The Pelagic Life in Fænø Sound etc. 1893. 38 pg. Tables.
- IV. Om vore Flynderfiskes Biologi og om vore Flynderfiskeriers Aftagen. 1894. 146 pg. 2 Tavler. 1 Kort og mange Tabeller.
- IV. On the Biology of our Flat-fishes and on the decrease of our Flat fish Fisheries. 1894. 146 pg. 2 Plates. 1 Chart. Many Tables.
- V. Den alm. Aal (*Anguilla vulgaris* T.) anlægger før sin Vandring til Havet en særlig Forplantningsdragt. 1896. 35 pg. Med 2 Tavler. Etc. 64 pg.
- V. The common Eel (*Anguilla vulgaris* T.) gets a Particular Breeding-dress before its Emigration to the Sea. 1896. 35 pg. With 2 Plates. Etc. 64 pg.
- VI. Om Rødspætteyngelens aarlige Indvandring i Limfjorden etc. 1887. 49 pg. 1 Kort. 2 Tabeller.
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 Report XIII. A. Otterstrøm.  
 — XIV, II. K. J. Gemzøe.  
 — XVI. C. H. Ostenfeld.





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