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## 6.—PLANKTONIC STUDIES: A COMPARATIVE INVESTIGATION OF THE IMPORTANCE AND CONSTITUTION OF THE PELAGIC FAUNA AND FLORA.

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[Translated by George Wilton Field.]

### TRANSLATOR'S PREFACE.

Prof. Hæckel's "Plankton-Studien" first appeared in the *Jenaische Zeitschrift*, vol. xxv, first and second parts, 1890. It was immediately published in separate form by Gustav Fischer, of Jena, and attracted much attention on the Continent and in England. The subject, "a comparative study of the importance and constitution of the marine fauna and flora," is presented in Prof. Hæckel's usual pleasing style, and the work can not fail to be of value to all interested in the biological sciences, to the general reader as well as to the specialist. It derives especial interest in connection with the work of the Fish Commission, from its broad discussion of those many important elements which enter into the food supply of all pelagic fishes, such as the mackerel and menhaden, and, considering the extensive physical investigations now being conducted in our coast waters by the schooner *Grampus*, its publication at the present time will prove exceedingly advantageous.

The terminology used by Prof. Hæckel may at first seem formidable, but this difficulty is more fancied than real. The terms are formed upon correct analogies, and most of them will probably find a permanent place. The definite restriction of the meaning of terms is a fundamental necessity in every science, and for the lack of this the branch of biology here considered is in a very unsatisfactory condition. The author, first of all, proposes certain terms with a definite meaning. The word "plankton," from the Greek  $\pi\lambda\alpha\gamma\tau\circ\varsigma$ , *wandering, roaming*, was, I believe, first employed by Hensen in place of the German "Auftrieb," to designate all plants and animals found at the surface of the ocean which are carried about involuntarily in the water. Hæckel adopts this term, but objects somewhat to the meaning at present attached to it.

Particularly valuable for us is the general review which the author gives of the discovery and growth of our knowledge of this branch,

which he names "planktology"; the distinctions which he points out between the varied constituents and distribution of the plankton; and finally his extremely valuable suggestions for further work in the field which he so justly terms "a wonder-land."

In the translation the liberty of omitting a few personal references was taken, for the reason that we in this country know very little of the facts which have called them forth.

In the case of several German words it has been found necessary for the sake of clearness to use a circumlocution. For instance, I can recall no English equivalent for "*Stoffwechsel des Meeres*," which would convey its meaning in a single word. The "cycle of matter in the sea," *i. e.*, the change of inorganic matter into vegetable and animal organic matter, and this finally again into inorganic matter, seemed the best rendering, though even this does not include all which the German term implies.

#### I.—HISTORICAL EXPLANATIONS.

For the great progress made in the last half century in our knowledge of organic life, we are indebted—next to the theory of development—in a great measure to the investigation of the so-called "pelagic animal world." These wonderful organisms, which live and swim at the surface of the sea and at various depths, have long aroused the interest of seafarer and naturalist, by the wealth of the manifold and strange forms, as well as by the astonishing number of individuals—these have been referred to in many old as well as in recent narratives. A considerable number of these, especially of the larger and more remarkable forms, were described and figured in the last, or in the first half of the present, century. The new and comprehensive investigation of the "pelagic world" began in the fifth decade of our century, and is therefore not yet 50 years old.

Into this, as into so many other regions of biology, the great Johannes Müller, of Berlin, equally distinguished in the realms of morphology and physiology, entered as a pioneer. He was the first who systematically and with great results carried on the "pelagic fishery by means of a fine net." In the autumn of 1845, at Helgoland, he began his celebrated investigations upon the development of echinoderms, and obtained the small pelagic larvae of the echinoderms, and other small pelagic animals living with them, as *sagitta*, worm larvae, etc., at first by "microscopical examination of the sea water, which was brought in" (1). This wearisome and thankless method was soon displaced by the successful use of the "fine pelagic net." In the treatise "on the general plan in the development of the echinoderms,"

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NOTE.—Citations inclosed in parentheses which occur in the text refer to the list of publications at the end of this paper (pp. 640, 641).

Müller compares the different methods of obtaining them, and chooses, above all, "fishing with a fine net at the surface of the sea." He says:

I have used this method for many years with the best results; for the advanced stages of the swimming larvae and for the time of maturity and metamorphosis it is quite indispensable, and in no way to be replaced.

The students who, in 1845-46, as well as in the following years, accompanied Johannes Müller to Helgoland and Trieste (Max Müller, Busch, Wilms, Wagener, and others) were introduced into this method of "pelagic fishery" and into the investigation of "pelagic tow-stuff" (*pelagische Auftrieb*) obtained thereby. It was soon employed at sea with excellent results by other zoölogists—by T. H. Huxley, by Krohn, Leuckart, Carl Vogt, and others, and especially by the three Würzburg naturalists, A. Kolliker, Heinrich Müller, and C. Gegenbaur, who in 1852 examined with such brilliant success the treasures of the Straits of Messina. At this time, in the beginning of the second half of our century, the astonishing wealth of interesting and instructive forms of life which the surface of the sea offers to the naturalist first became known, and that long series of important discoveries began which in the last forty years have filled so many volumes of our rapidly increasing zoölogical literature. A new and inexhaustibly rich field was thus opened to zoötomical and microscopical investigation, and anatomy and physiology, organology and histology, ontogeny and systematic zoölogy have been advanced to a surprising degree. The investigation of the lower animals has since then been recognized as a wide field of work, whose exploration is of great significance for all branches of science and to which we owe numberless spécial and the most important general conclusions.

The general belief of zoölogists regarding the extent of this rich pelagic animal world arose as the result of the discovery that a special "pelagic fauna" exists, composed of many characteristic forms, fundamentally different from the littoral fauna. This pelagic fauna is made up of animals (some floating passively, others actively swimming) which remain at the surface of the sea and never leave it, or only for a short time descend to a slight depth. Among such true "pelagic animals" are the radiolaria, peridinia, noctiluca, medusæ, siphonophores, ctenophores, sagitta, pteropods, heteropods, a greater part of the crustacea, the larvae of echinoderms, of many worms, etc.

Important changes were first made in the prevailing idea of the "pelagic fauna" by the remarkable discoveries of the epoch-making *Challenger* expedition (1873-1876). The two leaders of this, Sir Wyville Thompson and Dr. John Murray, did not limit themselves to their chief object, the general physical and biological investigation of the deep sea, but studied with equal care and perseverance the conditions of organic life at the surface of the ocean and in zones of

various depths. As the most significant general result Murray, in his "Preliminary Report" (1876), says:

Everywhere we have found a rich organic life at and below the surface of the ocean. If living individuals are scarce at the surface, below it the tow net commonly discloses numerous forms, even to a depth of 1,000 fathoms and more (5, p. 536).

In 1875, on the journey through the North Pacific Ocean (from Japan to the Sandwich Islands), the extremely important fact was established that the pelagic organisms in oceanic zones of different depths belong to different species; fine pelagic nets (or tow nets) "on many occasions were let down even to depths of 500, 1,000, and 2,000 fathoms, and thereby were discovered many swimming organisms which had never been captured hitherto, either at the surface of the ocean or at slight depths (up to 100 fathoms below the surface)" (6, p. 758). The most characteristic forms of these zones of different depths belong chiefly to the class of the *Radiolaria*, especially to the order of the *Phaeodaria*.

Through the investigation of the *Challenger* radiolaria, which occupied for ten years the greater part of my time and attention, I was led to study anew these conditions of distribution; and I reached the conviction that the differences discovered by Murray in the pelagic fauna, at different depths of the ocean, were still more significant than he assumed, and that they had the greatest significance, not merely for the radiolaria, but also for other groups of swimming oceanic organisms. In 1881, in my "Entwurf eines Systems der Challenger Radiolarien," p. 422, I distinguished three groups: (a) pelagic, living at the surface of the calm sea; (b) zonary, living in distinct zones of depth (to below 20,000 feet); and (c) profound (or abyssal) animals living immediately above the bottom of the deep sea. In general, the different characteristic forms correspond (to below 27,000 feet) to the different zones.

In my "General Natural History of the *Radiolaria*" (4, p. 129) I have established this distinction, and have expressed my conviction that it is possible, by the aid of a suitable bathygraphic net, to demonstrate many different faunal belts overlying one another in the great deep-sea zones.

The existence of this "intermediate pelagic fauna," discovered by Murray, inhabiting the zones of different depths of the ocean between the surface and the deep-sea bottom, which I have briefly called "zonary fauna," has been decidedly contradicted by Alexander Agassiz. He claimed, on the ground of "exact experiments" carried on during the *Blake* expedition, in 1878, that the greater part of the ocean contains absolutely no organic life, and that the pelagic animals go down no deeper than 100 fathoms. "The experiments finally show that the surface fauna of the sea is actually limited to a relatively thin layer, and that no intermediate zone of animal life, so to speak, exists between the fauna of the sea bottom and of the surface" (15, pp. 46, 48).

Although these negative conclusions from the so-called "exact experiments" of Agassiz are contradicted by the foregoing results of the *Challenger* investigator, yet against the latter, with some show of right, Agassiz might have raised the objection that the "tow net" used could establish no safe conclusion.\* This objection could only be finally removed by the construction of a new tow net, which could be let down closed to a certain depth, and then opened and closed again. The merit of inventing such a closable net, and of the immediate successful use of it, belongs to two distinguished Italian naval officers: G. Palumbo, commander of the Italian war corvette *Vettor Pisani*, first constructed such a closable pelagic net or "bathygraphical zone net;" and Naval Lieutenant Gaetano Chierechia, who during the three years' voyage of the *Vettor Pisani* around the world made a very valuable collection of pelagic animals, used the new closable net with fine results, even at a depth of upwards of 4,000 meters (8, p. 83).

Chierechia's first trial with this "deep-sea closable net" was June 5, 1884, in the East Pacific Ocean, directly under the equator,  $15^{\circ}$  west of the Galapagos Islands. Fourteen days later, June 19, midway between the Galapagos and the Sandwich Islands, this closable net was sunk to 4,000 meters. In this and in many other trials these Italian naval officers captured an astonishing wealth of new and interesting zonary animals, whose description has for a long time busied zoölogists. The collections brought back to Naples by the *Vettor Pisani* are, next to those of the *Challenger*, the most important materials from the region under consideration.

A few faults which pertained to Palumbo's net were soon done away with by improvements, for which we are indebted to the engineer Petersen and to Prof. Carl Chun, of Breslau. The latter, in 1886, made trials in the Gulf of Naples with the improved closable net which showed "a still more astonishing richness of pelagic animals in greater

\* The "tow nets" used by the *Challenger* were the ordinary Müller's net (or the "fine pelagic net" of Joh. Müller), a round bag of Müller gauze or silk mull, the mouth being kept open by a circular metallic ring. This ring is in ordinary pelagic fishing fastened to a handle 2 or 3 meters long (like the ordinary butterfly net). While the boat moves along, the opening of this net is held at the surface in such a way that the swimming animals are taken into the bag. They remain hanging in the bottom of this, while the water passes through the narrow meshes of the net. After a time the net is carefully inverted and the tow stuff (*Auftrieb*) is emptied into a glass vessel filled with sea water. If one wishes to fish below the surface, the ring of the net is fastened by means of three strings, equally distant from one another, which at a point (about 1 meter distant from the opening of the net) are joined to a longer line which is sunk by weights to a definite distance, corresponding to the desired depth. When Murray fastened such a tow net to the deep-sea sounding line or to the long line of the deep-sea dredge, he first obtained the inhabitants of the "intermediate ocean zones," but he could not thereby avoid the objection that, since this tow net always remained open, the contents might come from very different depths or even only from the surface. For in drawing up the open tow net animals from the most different zones of depth might occasionally be taken in.

depths, and completely overthrew the assumption that an azoic layer of water exists between the surface and the sea bottom" (15, p. 2). Chun embraced the general results of his important bathypelagic investigations under the four following heads:

- (1) The portion of the Mediterranean investigated showed a rich pelagic fauna at the surface as well as at all depths up to 1,400 meters.
- (2) Pelagic animals which during the winter and spring appear at the surface seek deep water at the beginning of summer.
- (3) At greater depths occur pelagic animals which have hitherto been seldom or never observed at the surface.
- (4) A number of pelagic animals also remain at the surface during the summer, and never sink into deep water (15, p. 44).

Among the remarks which Chun made on the vertical distribution of the pelagic fauna and the astonishing planktonic wealth of the depths of the sea (at 1,000 to 2,000 meters), he justly throws out the question, "Who knows, whether in the course of time our views will not undergo a complete reversal, and whether the depths will not show themselves as the peculiar mother earth of pelagic life, from which, for the time being, swarms are sent out to the surface as well as to the sea bottom! There are only a few forms which can so completely adapt themselves to the changing conditions of existence at the surface that they no more seek the deeper levels" (15, p. 49). In consequence of his observations on the periodic rising and sinking of pelagic animals, Chun "can not resist the impression that from the abundance of animal life in the depths the surface fauna represents relatively only an advance guard of the whole, which sometimes to a greater, sometimes to a less extent, and occasionally completely, withdraws itself into more protected regions. Facts plainly speak for this, that the periodical wandering of pelagic animals in the vertical direction is especially conditioned by the changes in temperature. Only a few pelagic animal groups can endure the high temperature of the surface water during the summer; the majority withdraw from the influence of this by sinking, and, finally, whole groups pass their life in the cool deep regions without ever rising to the surface" (15, p. 54).

The general ideas which Chun had obtained by this deep-sea investigation of the Mediterranean he was able to confirm for the Atlantic Ocean on a trip made in the winter of 1887-88 to the Canary Islands (16, p. 31). At this time he made the observation that the periodical wandering of pelagic animals in a vertical direction was influenced in great part by ocean currents (at the surface as well as in deep water), and that among other things the occurrence of the full moon exerted a significant action (16, p. 32). Chun's special observation in the sea of Orotava, upon the poverty of the Canary plankton in November and December and the sudden appearance of great numbers and many species of pelagic animals in January and February, agrees completely with the observations which I myself made twenty years before at

the Canary island Lanzarote. I also entirely agree with Chun in regard to his general views upon the chorology of the plankton, and consider his investigations upon the pelagic animal world and its relation to the surface fauna as the most important contribution which planktology has received since the pioneer discoveries of the *Challenger* and of the *Vettor Pisani*.

Entirely new aspects and methods have been introduced into pelagic biology in the last three years by Dr. Victor Hensen, professor of physiology at Kiel (9 and 22). He has for a number of years thoroughly studied the conditions of life of the fauna and flora of the bay of Kiel, and as a member of the commission for the scientific investigation of the German Ocean (at Kiel) has endeavored to improve and extend the fisheries there, and by counting the fish eggs collected to get an approximate idea of the number of fish in corresponding districts (9, p. 2). This investigation led him to the conclusion that it was necessary and possible to come nearer to the fundamental food supply of marine animals and to determine this quantitatively. For solving this problem Hensen invented a new mathematical method (2, p. 33). He constructed a new pelagic net (p. 3), and in July, 1884, in company with three other naturalists of Kiel, undertook a nine-day excursion in the North Sea and Atlantic Ocean, which was extended to the Hebrides and to the Gulf Stream ( $57^{\circ} 42' N.$  Lat.) (p. 30). In 1887 he published the results of this investigation in a comprehensive work containing many long numerical tables, "On the Determination of the Plankton, or the Animal and Vegetable Material found in the sea" (9). He used the term "plankton" in place of "Auftrieb," the word hitherto commonly used, because this name is not sufficiently comprehensive and suitable (9, p. 1). To be sure, the German term "Auftrieb" or "pelagischer Mulder," introduced by Johannes Müller forty years ago, was in general use and has many times been used in English, French, and Italian works. But I agree with Hensen that in this, as in other scientific terms, a Greek *terminus technicus*, capable of easier flexion, is preferable. I adopt the term Plankton in place of "Auftrieb," and form from it the adjective planktonic (*planktonisch*). The whole science which treats of this important division of biology is briefly called planktology.

Hensen regards the *mathematical determination of the plankton* as the chief aim of planktology from a physiological standpoint. By it he hopes to solve the somewhat neglected question of the cycle of matter in the sea. For the purpose of solving this, and to make a trial of his new method on a larger scale, Hensen, in the summer of 1889, arranged a more extensive expedition in the Atlantic, which was most liberally supported by the German government and by the Berlin Academy of Sciences. The German Emperor furnished 70,000 marks; the Berlin

Academy gave, from the income of the Humboldt fund, 24,600 marks, and by further contributions the entire sum at the disposal of the expedition was raised to 105,600 marks—a sum never before made available in Germany for a biological expedition. The new steamer *National*, of Kiel, was chartered for three months, and was fitted out "with all the admirable contrivances for obtaining plankton, for deep-sea fishing, and for sounding." Besides the leader of the expedition, Prof. Hensen, five other naturalists participated: the zoölogists Brandt and Dahl; the botanist Schütt; the bacteriologist Fischer; the geographer Kriimmel; and the marine artist Richard Eschke. The voyage of the *National* lasted 93 days (July 7 to November 15). The course was westward through the north Atlantic (Gulf Stream, Sargasso Sea), then southward (Bermudas, Cape Verde, Ascension) to Brazil, and eastward back by the Azores. During this voyage 400 casts were made, 140 with the plankton nets, 260 with other nets.

Our German navy has been but little used for scientific, still less for biological, investigations; much less than the navies of England, France, Italy, Austria, and the United States. The remarkable services which many distinguished German zoölogists have rendered in the last half-century for the advancement of marine biology have been carried on almost entirely without government aid. The German government has hitherto had very little means available for this branch of science. Therefore, great was the satisfaction when, by the liberal endowment of the plankton expedition of Kiel, the first step was taken for the more extensive investigation, with better apparatus, of the biology of the ocean, and for emulation of the results which the English *Challenger* and the Italian *Vettor Pisani* had lately obtained in this region.

Accounts have been published of the results of the plankton expedition of Kiel, by Victor Hensen (22), Karl Brandt (23), E. du Bois Reymond (21), and Kriimmel. The essential details of these accounts have been repeatedly published in the German newspapers, to the general effect that the proposed goal was reached and the most important question of the plankton was happily solved. I very greatly regret that I can not agree with this favorable verdict. (1) The most important generalizations which the plankton expedition of Kiel obtained on the composition and distribution of the plankton in the ocean stand in sharp contradiction to all previous experience; one or the other is wrong. (2) It seems to me that Hensen has incantiously founded a number of far-reaching erroneous conclusions on very insufficient premises. Finally, I am convinced that the whole method employed by Hensen for determining the plankton is utterly worthless, and that the general results obtained thereby are not only false, but also throw a very incorrect light on the most important problems of pelagic biology. Before I establish this dissenting opinion let me give an account of my own planktonic studies and their results.

## II.—PLANKTONIC STUDIES.

My own investigations on the organisms of the plankton were begun thirty-six years ago, when I got my first conception of the wonderful richness of the marine fauna and flora in the North Sea. Accepting the kind invitation of my ever-remembered teacher, Johannes Müller, I accompanied him in the autumn of 1854 on a vacation trip to Helgoland, and was introduced by him personally into the methods of plankton fishery and the investigation of the pelagic fauna. There, during August and September, I accompanied him daily on his boating trips, and under all conditions of the rich planktonic captures I received from him the most competent instruction, and pressed with corresponding eagerness into the mysteries of this wonderful world. Never will I forget the astonishment with which I first beheld the swarms of pelagic animals which Müller emptied by inversion of his "fine net" into a glass jar of sea water—a confused mass of elegant medusæ and glistening ctenophores, swift-darting sagittas and snake-like tomopteris, copepods and schizopods, the pelagic larvae of worms and echinoderms. The important stimulus and instruction of the founder of planktonic investigation has exercised a constant influence on my entire later life, and has given me a lasting interest in this branch of biology.\*

Two years later (in August and September, 1856), while at Würtzburg, I accepted the invitation of my honored teacher, A. Kölliker, to accompany him to Nizza, and, under his excellent guidance, became acquainted with the zoölogical treasures of the Mediterranean. In company with Heinrich Müller and K. Kupffer, we investigated especially the rich pelagic animal life of the beautiful bay of Villafranca. There, for the first time, I met those wonderful forms of the pelagic fauna which belong to the classes of the siphonophores, pteropods, and heteropods. I also there first saw living polycyttaria, acanthometra, and polycystina, those phantasmic forms of radiolaria, in the study of which I spent so many later years.

Johannes Müller, who was at this time at Nizza, and had already begun his special investigation of this latter order, called my attention to the many and important questions which the natural history of these enigmatical microscopical organisms present. These valuable suggestions resulted some years later in my going to Italy and spending an entire year in pelagic fishing on the Mediterranean coast. Dur-

\* When at Helgoland, investigating the wonders of the plankton with the microscope, Johannes Müller, pleased with the care and patience with which his zealous students tried to study the charming forms of medusæ and ctenophores, spoke to me the ever-memorable words, "There you can do much; and as soon as you have entered into this pelagic wonderland you will see that you can not leave it."

ing the summer of 1859, at Naples and at Capri, I endeavored to gain as wide a knowledge as possible of the marine fauna. In the following winter, at Messina, I devoted my entire attention to the investigation of the radiolaria, and thus obtained the material which forms the basis of my monograph of this class (1862). Daily boat trips in the harbor of Messina made me acquainted with all the forms in the pelagic fauna which make this classic spot, in consequence of the combination of uncommonly favorable conditions, far richer for planktonic study and investigation than any other point on the Mediterranean (3, pp. v, 25, 166, 170).

For a full generation, since that time, the study of plankton has remained my most pleasant occupation, and I have hardly let a year pass without going to the seacoast and, by means of the pelagic net, getting new material for work. Various inducements were offered to me in addition; on the one hand the radiolaria, on the other the siphonophores and medusæ, to which I had already given some attention while at Nizza in 1864. The results of these studies are given in my monographs of these two classes (1879 and 1888). In the course of these three decades I have by degrees become acquainted with the entire coast of the Mediterranean and its fauna. I have already made reference, in the preface to my "System of Medusæ," p. xvi, to the places where I have studied this subject. In addition to the Mediterranean I have continued my planktonic studies on the west coast of Norway (1869); on the Atlantic coast of France (1878); on the British coast (1876 and 1879); at the Canary Islands (1866-67); in the Red Sea (1873), and in the Indian Ocean (1881-82).

By far my richest results and my deepest insight into the biology of the plankton were vouchsafed me during a three months' residence at Puerto del Arrecife, the seaport of the Canary island Lanzarote (in December, 1886, and in January and February, 1887). The pelagic fauna in this part of the Atlantic is so rich in genera and species; the fabulous wealth of life in the wonderful "animal roads" or Zain currents (18, p. 309) is, every day, so great, and the opportunities for investigation on the spot are so favorable that Lanzarote afforded me greater advantages for planktonic study than all the other places ever visited by me (excepting perhaps Messina). Every day the pelagic net brought to me and to my companions (Prof. Richard Greeff and my two students, N. Miklueho-Maclay and H. Fol) such quantities of valuable tow-stuff (*Auftrieb*) that we were able to work up only a very small part of it. At that time I concentrated my chief interest on the medusæ and siphonophores, and the larger part of the new material which is worked up in my monographs of these two classes was collected at Lanzarote. All my observations "On the Development of the Siphonophores" (1869) were made there.

The excursion to the coral reefs of the Red Sea (1873), which is recounted in my "Arabic Corals," and the trip to Ceylon, about which I have written in my "Indian Journal" (*Indische Reisebriefe*, 1882), were extremely valuable to me, because I thereby gained an insight into the wonders of the Indian fauna and flora. On the journey from Suez to Bombay (in November, 1881), as well as on the return from Colombo to Aden (in March, 1882), I was able to make interesting observations on the pelagic fauna of the Indian Ocean, as well as during a six weeks' stay at Belligan and in the pelagic excursions which I made from there. I obtained thereby a living picture of the oceanic and neritic fauna of the Indo-Pacific region, which differs in so many respects from that of the Atlantic-Mediterranean region. The special results of my experience there are, with the kind consent of Dr. John Murray, for the most part embraced in my report on the Radiolaria (1887), and on the Siphonophora (1888), which form parts XVIII and XXVIII of the *Challenger Report*. These two monographic reports also contain many observations on plankton, which I had made in earlier journeys and had not yet published.

The extensive experience which I had gained through my own observations of living plankton during a period of three decades was well filled out by the investigation of the large and well-preserved planktonic collections placed at my disposal from two different sources by Capt. Heinrich Rabbe, of Bremen, and by the *Challenger* directors of Edinburgh. Capt. Rabbe, with very great liberality, turned over to me the valuable collection of pelagic animals which he had obtained on three different trips (with the ship *Joseph Haydn*, of Bremen) in the Atlantic, Indian, and Pacific oceans, and which he had carefully preserved according to my directions and by approved methods. This extraordinarily rich and valuable material, contained in numerous bottles, embraced planktonic samples from the most diverse localities of the three oceans, chiefly in the southern hemisphere. Like the much more extensive collection of the *Challenger*, it gives (though to a smaller degree) a complete summary of the complexity of the composition of the plankton and the difference in its constituents. Rabbe's collection supplements that of the *Challenger* in a most welcome manner, since the course of the *Challenger* was southward from the Indian Ocean through the Antarctic region, and between the Cape of Good Hope and Melbourne was always south of 40° south latitude. The course of the *Joseph Haydn*, on the other hand, on the repeated voyages through the Indian Ocean, was much more northerly, and between Madagascar, the Cocos Islands, and Sumatra included a number of points where the pelagic net obtained a very rich and peculiarly constituted capture. I hope to be able to publish soon in detail the special results which I have obtained by investigation of Rabbe's plankton collection, with the aid of the carefully kept journal which Capt. Rabbe made of his observations. The discoveries of new radiolaria, medusæ, and siphonophores

which I owe to these are already embraced in my monographs on these three classes in the *Challenger* Report, and in the preface I have expressed to Capt. Rabbe my sincere thanks for his very valuable aid.

Of all expeditions which have been sent out for investigating the biology of the ocean, that of the *Challenger* was, without doubt, the greatest and the most fruitful, and I recognize it with additional gratitude since I was permitted for twelve years to take part in working up its wonderful material. When, after the return of the expedition, I was honored by its leader, Sir Wyville Thompson, by being summoned to work up the extensive collection of radiolaria, I believed, after a hasty survey of the treasures, that I could complete their investigation in the course of three to five years; but the further I proceeded in the investigation the greater seemed the assemblage of new forms (4, p. xv), and it was a whole decade before the report on the radiolaria (part XVIII) was completed. Three other reports were also then finished—on deep-sea horny sponges (part LXXXII), on the deep-sea medusæ (part XII), and on the siphonophores (part XXVIII) collected by the *Challenger*. The comparative study of these extremely rich planktonic treasures was highly interesting and instructive, not only on account of the daily additions to the number of new forms of organisms in these classes, but also because my general ideas on the formation, composition, and importance of the plankton were enriched and extended. I am sincerely thankful for the liberality with which Sir Wyville Thompson, and after his untimely death (1882) his successor, Dr. John Murray, placed these at my entire disposal.

A record of the 168 stations of observations of the *Challenger* expedition, whose soundings, plankton results, and surface preparations I have been able to investigate, has been given in § 240 of the report on the radiolaria (4, p. CLX). The number of the bottles containing plankton (from all parts of the ocean) in alcohol amounts to more than a hundred, and in addition there are a great number of wonderful preparations which Dr. John Murray finished at the different observation stations, stained with carmine and mounted in Canada balsam. A single such preparation (for example, from station 271) contains often 20 to 30 and sometimes over 50 new species. Since the material for these preparations was taken with the tow net, not only from the surface of all parts of the sea traveled by the *Challenger*, but also from zones of different depths, they make important disclosures in morphology as well as in physiology and chorology. To the study of these station preparations I am indebted for many new discoveries. I have been able to examine over a thousand (4, p. 16).

If I here refer to the development and extension of my own plankton studies, it is because I feel compelled to make the following brief summary of results. I am not now in a position to give the proofs in detail, and must defer the thorough establishment of the most weighty

series of observations for a later and more detailed work. But since, to my regret, I am compelled to decidedly contradict the far-reaching assertions made by Hensen (22), it is only to justify and prove these that I refer to my extended experience of many years. I believe I do not err in the assumption that among living naturalists I am one of those who by extensive investigation on the spot have become most thoroughly acquainted with the conditions of the plankton and have worked deepest into these intricate problems of marine biology. If I had not for so many years had these continually in mind, and at each new visit to the sea begun them anew, I would not dare to defend with such determination the assertions expressed in the following pages.

### III.—CHOROLOGICAL TERMINOLOGY.

The science of the distribution and division of organic life in the sea (marine chorology) has in the last decade made astonishing progress. Still this new branch of biology stands far behind the closely related terrestrial chorology, the topography and geography of land-dwelling organisms. We have as yet no single work which treats distinctly and comprehensively of the chorology of marine plants and animals in a manner similar to Griesbach's "Vegetation of the Earth" (1872) for the land plants, and Wallace's "Geographical Distribution of Animals" (1876) for the land animals.

How much there is still to be done is shown by the fact that not one of the simplest fundamental conceptions of marine chorology has yet been established. For example, the most important conception of one subject, that of the pelagic fauna and flora, is now employed in three different senses. Originally, and through several decades, this term was used only in the sense in which Johannes Müller used it, for animals and plants which are found swimming at the surface of the sea. Then the term was extended to all the different animals and plants which are found at the surface of fresh-water basins. It was so used, for example, by A. Weismann in his lecture upon "the animal life at the sea-bottom" (1877), in which he "distinguishes the animal world living on the shore from the 'pelagic or oceanic company living in the open sea.'" To a third quite different meaning has the conception of the pelagic living world been widened by Chun (1887), who extends it from the surface of the ocean down to the greatest depths (15, p. 45). In this sense the conception of the pelagic organisms practically agrees with the "plankton" of Hensen.

Errors have already arisen from the varied use of such a fundamental conception, and it seems necessary to attempt to clear this up, and to establish at least the most important fundamental conception of marine chorology. In the use of words I will, as far as possible, conform to the usage of the better authors.

## MARINE FLORA AND FAUNA.

Since the old mooted question about "the limits of the animal and vegetable kingdom" comes anew into the foreground in the planktonic studies, a few words must first be devoted to its consideration. In the plankton, those organisms (for the most part microscopic) which stand on the boundary line and which may be regarded as examples of a neutral "Protista realm," play a conspicuous part—the unicellular diatoms and muraeocytes, dictyocha and palmellaria, thalamophora and radiolaria, dinoflagellata and cystoflagellata. Since it is still asserted that for replies to this boundary question we need new researches, "more exact observations and experiments," I must here express the opposing belief, that the desired answer is not to be obtained by this empirical and inductive method, but only by the philosophic and deductive method of more logical definite conception (*logischer Begriff-Bestimmung*). Either we must use as a definite distinction between the two great organic realms the physiological antithesis of assimilation, and consider as "plants" all "reducing organisms" (with chemical-synthetic functions) and as "animals" all "oxidizing organisms" (with chemical-analytical functions) or we may lay greater weight on the morphological differences of bodily structure and place the unicellular "*Protista*" (without tissues) over against the multicellular *Histona* (with tissues).\*

For the problem before us, and with more particular reference to the important questions of the fundamental food supply (*Urnahrung*) and the cycle of matter in the sea (*Stoffwechsel des Meeres*), it is here more suitable to employ the first method. I regard the diatoms, muraeocytes, and dinoflagellates as *Protophytes*, the thalamophores, radiolarians, and cystoflagellates as *Protozoa*.

For a term to designate the totality of the marine flora and fauna, the expression *halobios* seems to be suitable, in opposition to *limnobios* (the organic world of fresh water) and to *geobios* (as the totality of the land-dwelling or terrestrial plant and animal world). The term *bios* was applied by the father of natural history, Aristotle, "to the whole world of living" as opposed to the lifeless forms, the *abion*. The term biology should be used only in this comprehensive sense, for the whole organic natural science, as opposed to the inorganic, the abiology. In this sense, zoölogy and botany on the one side, and morphology and physiology on the other, are only subordinate parts of biology, the general science of organisms. But if (as is frequently done to-day even in Germany) the term biology is used in a much narrower sense, instead of *ecology*, this narrowing leads to misunderstandings. I mention

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\* *Protista* and *Histona* may both again be divided into two groups, on the ground of the different assimilation, into an animal and a vegetable group, the *Protista* into *Protophyta* and *Protozoa*, the *Histona* into *Metaphyta* and *Metazoa*. Compare my "Natural History of Creation" (*Natürliche Schöpfungsgeschichte*), 8th edition, 1889, pp. 420 and 453.

this here because in planktology the interesting and complex, vital relations of pelagic organisms, their manner of life and economy, are very often called biological instead of ecological problems.\*

#### PLANKTON AND BENTHOS.

If under the term *Halobios* we embrace the totality of all organisms living in the sea, then these, in ecological relation, fall into two great chief groups, *benthos* and *plankton*. I give the term *benthos*† (in opposition to *plankton*) to all the non-swimming organisms of the sea, and to all animals and plants which remain upon the sea bottom either fixed (sessile) or capable of freely changing their place by creeping or running (vagrant). The great ecological differences in the entire mode of life, and consequently in form, which exist between the benthonic and planktonic organisms, justify this intelligible distinction, though here as elsewhere a sharp limit is not to be drawn. The *benthos* can itself be divided into littoral and abyssal. The *littoral-benthos* embraces the sessile and vagrant marine animals of the coast, as well as all the plants fixed to the sea-bottom. The *abyssal-benthos*, on the other hand, comprises all the fixed or creeping (but not the swimming) animals of the deep sea. Although as a whole the morphological character of the *benthos*, corresponding to the physiological peculiarities of the mode of life, is very different from that of the *plankton*, still these two chief groups of the *halobios* stand in manifold and intimate correlation to one another. In part these relations are only phylogenetic, but also in part at the present day of an ontogenetic nature, as, for example, the alternation of generations of the benthonic polyps and the planktonic medusae. The adaptation of marine organisms to the mode of life and the organization conditioned thereby may in both chief groups be primary or secondary. These and other relations, as, well as the general characteristics of the pelagic fauna and flora, have already been thoroughly considered by Fuchs (12) and Moseley (7).

#### PLANKTON AND NEKTON.

The term *plankton* may be used in a wider and in a narrower sense; either we understand it as embracing all organisms swimming in the sea, those floating passively and those actively swimming; or we may exclude these latter. Hensen comprehends under *plankton* "everything which is in the water, whether near the surface or far down, whether dead or living." The distinction is, whether the animals are driven involuntarily with the water or whether they display a certain degree of independence of this impetus. Fishes in the form of eggs

\* The terms biology and ecology are not interchangeable, because the latter only forms a part of physiology. Comp. my "Generelle Morphologie," 1866, Bd. I, p. 8, 21; Bd. II, p. 286; also my "Ueber Entwicklungsgang und Aufgabe der Zoölogie," Jena. Zeitsch. für Med. u. Nat., Bd. V, 1870.

† *βέρθος*, the bottom of the ocean; hence the organisms living there.

and young belong in the highest degree to the plankton, but not when mature animals. The copepods, although lively swimmers, are tossed about involuntarily by the water, and, therefore, must be reckoned in the plankton (9, p. 1). If, with Hensen, we thus limit the conception of *plankton*, then we must distinguish the *actively* swimming *nekton* from the *passively* driven *plankton*. The term thus loses its firm hold, and becomes dependent on quite variable conditions; upon the changing force of the current in which the animal is driven, by the momentary energy of voluntary swimming movements, etc. A pelagic fish or copepod, which is borne along by a strong current, belongs to the plankton; if he can make a little progress across this current, and if, besides this, he can voluntarily and independently define his course, then he belongs also to the nekton. It therefore seems to me advisable, as preliminary, to regard the term plankton in the wider sense, in opposition to benthos.

Still, for the chief theme which Hensen has set up in his plankton studies, for the physiological investigation of the cycle of matter in the sea (*Stoffwechsel des Meeres*), this limitation of the plankton conception will not hold; for a single large fish which daily devours hundreds of pteropods or thousands of copepods exerts a greater influence on the economy of the sea than the hundreds of small animals which belong to the plankton. I will return to this in speaking of the vertebrates of the plankton. If with Hensen we could, on practical grounds, separate those animals of the plankton which are carried involuntarily from those following their own voluntary swimming movements (independent of the current), we might distinguish the former as *ploteric*,\* the latter as *necteric*.\*

#### HALIPLANKTON AND LIMNOPLANKTON.

Although the swimming population of fresh water shows far less variety and peculiarity than that of the sea, still among the former as among the latter similar conditions are developed. Already the study begins to take a joyous flight to the pelagic animals of the mountain lakes, etc. Therefore, it will be necessary here also to fix limits, as has been already done for the marine fauna; but since the term "pelagic" should only be used for marine animals, it becomes advisable to designate as *limnetic* the so-called "pelagic" animals of fresh water. Among these we can again distinguish *autolimnetic* (living only at the surface), *zonolimnetic* (limited to certain depths), and *bathylimnetic* (dwellers in the deep waters). The totality of the swimming and floating population of the fresh water may be called *limnoplankton*, as opposed to the marine *haliplankton* (9, p. 1), which we here briefly call *plankton*.

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\* Ηλιότης = drifting; νηκτής = swimming.

## OCEANIC AND NERITIC\* PLANKTON.

The manifold differences which the character of the plankton shows according to its distribution in the sea, lead first, with reference to its horizontal extension, to a distinction between oceanic and neritic plankton. *Oceanic plankton* is that of the open ocean, exclusive of the swimming *bios* of the coast. The region of oceanic plankton may from a zoölogical point of view be divided into five great provinces: (1) the Arctic Ocean; (2) the Atlantic; (3) the Indian; (4) the Pacific; (5) the Antarctic. In each of these five great provinces the characteristic genera of the plankton are apparent through the different species, even if the differences in general are not so significant as in the different provinces of the neritic and still more of the littoral fauna.

The neritic plankton embraces the swimming fauna and flora of the coast regions of the continents as well as the archipelagos and islands. This is in its composition essentially different from the oceanic plankton, and is quantitatively as well as qualitatively richer. For along the coast there develop, partly under protection of the littoral *bios*, or in genetic relation with it, numerous swimming animal and vegetable forms which do not generally occur in the open ocean, or there quickly die; but the floating organisms of the latter may be driven by currents or storms to the coast and there mingled with the neritic plankton. Aside from this the richness of the neritic plankton in genera and species is much greater than that of the oceanic. The complicated and manifold relations of the latter to the former, as well as the relations of both to the benthos (littoral as well as abyssal), have been but little investigated and contain a fund of interesting problems. One could designate the neritic plankton also as "littoral plankton" if it were not better to limit the conception of the littoral *bios* to the non-swimming organisms of the coast, the vagrant and sessile forms.

## PELAGIC, ZONARY, AND BATHYBIC PLANKTON.

I keep the original meaning of the *pelagic plankton* as given forty-five years ago by Johannes Müller, and used since by the great majority of authors. I also limit the meaning of the pelagic fauna and flora to those actively swimming or passively floating animals and plants, which are taken swimming at the surface of the sea, no matter whether they are found here alone or also at a variable depth below the surface. These are the *superficial* and *interzonary* organisms of Chun (15, p. 54). On the other hand, I distinguish the *zonary* and *bathybic* organisms; I call *zonary plankton* those organisms which occur only in zones of definite depths of the ocean, and above this (at the surface of the sea) or below (at the sea bottom) are only found occasionally, as for example many phaeodaria and crustacea; also the deep-sea siphonophores dis-

\* Νηρίτης, son of Nereus.

covered by Chierchia, which were taken by him in great numbers and in great vertical and horizontal extension, but never higher than 1,000 meters below the surface and never deeper than 1,000 meters above the sea bottom (8, p. 85). The deepest part of this zonary fauna forms the *bathybie plankton* (or the profound tow-stuff, *Auftrieb*), *i. e.*, animals of the deep sea, which only hover over the bottom but never touch it, whether they stand in definite relation to the abyssal benthos or not. One might also call them "*abyssal plankton*," if it were not more practicable to limit the term "*abyssal*" to the (vagrant and sessile) benthos of the deep sea. To the bathybie plankton belong many phaeodaria, some medusæ and siphonophores, many deep-sea crustacea, *Tomopteris euchata*, *Megalocereus abyssorum*, etc. (15, pp. 55-57).

In each of these vertical parts of the plankton, distinctions may be made which apply to the *horizontal* distribution. We may also distinguish oceanic and neritic forms in the pelagic fauna as in the zonary and bathybie fauna.

#### AUTOPELAGIC, BATHYPELAGIC, AND SPANIPELAGIC PLANKTON.

If, following the old custom, we limit the term "*pelagic bios*" to those organisms which, at some time, swim or float at the *surface* of the sea—if we do not with Chun (15, p. 45) extend this term to the zonary and bathybie animals—it still is necessary to further distinguish by different terms those forms of life which constantly, temporarily, or only exceptionally live at the surface of the sea. I suggest for these the terms autipelagic, bathypelagic, and spanipelagic. *Autipelagic* are those animals and plants which are constantly found only at the surface (or in stormy weather at slight depths below it), the "*superficial*" of Chun (15, pp. 45, 60). To this "*constant superficial fauna*" belong, for example, many polycyttaria (most sphaeropods), many medusæ (*e. g.*, *Eucopidae*), and many siphonophores (*e. g.*, *Forskalidæ*); further, the lobate etenophores (*Eucharis*, *Bolina*), particular species of *Sagitta* (*e. g.*, *bipunctata*), and many copepods (*e. g.*, *Pontellina*, 15, p. 27).

I call *bathypelagic* all those organisms which occur not merely at the surface, but also extend down into the depths, and often fill the deep layers of the ocean in not less astonishing multitudes than the surface layers. Chun designates such bathypelagic animals as "*interzonary pelagic animals*" (15, p. 45). Here belongs properly the chief mass of the plankton; for through the agreeing researches of Murray (5, 6), Moseley (7), Chierchia (8), and Chun (15, 16), as well as from my own wide experience, it becomes highly probable that the great number of pelagic animals and plants only pass a part of their lives at the surface; swimming at different depths during the other part. Among the bathypelagic animals there are farther to be distinguished: (*a*) *Nyctipelagic*, which arise to the surface only at night, living in the depths during the day; very many medusæ, siphonophores, pyrosoma, most

pteropods, and heteropods, very many crustacea, etc.; (b) *Chimopelagic*, which appear at the surface only in winter and in summer are hidden in the depths—radiolaria, medusæ, siphonophores, ctenophores, a part of the pteropods and heteropods, many crustacea, etc.; (c) *Allopelagic*, which perform irregular vertical wanderings, sometimes appearing at the surface, sometimes in the depths, independently of the changes of temperature, which condition the change of abode of the nyctipelagic and chimopelagic animals; the final cause of these wanderings ought to be found in different oecological conditions, as of reproduction, of ontogeny, of food supply, etc.

Finally one may call *spanipelagic* those animals which always live in the ocean depths (zonary or bathybic), and come to the surface only exceptionally and rarely. This does not apply to a few deep-sea animals which once every year ascend to the surface, but only for a short time, for a few weeks or perhaps for a single day, e. g., *Athorybia* and *Physophora* among the siphonophores, *Charybdea* and *Periphylla* among the medusæ. The final cause of this remarkable spanipelagic mode of life must lie chiefly in the conditions of reproduction and ontogeny. These animals must be much more numerous than present appearances show.

#### HOLOPLANKTONIC AND MEROPLANKTONIC ORGANISMS.

Numerous organisms pass their whole life and whole cycle of development hovering in the ocean, while with others this is not the case. These rather pass a part of their life in the benthos, either vagrant or sessile. The first group we call *holoplanktonic*, and the second *meroplanktonic*. To the holoplanktonic organisms, which have no relation whatever to the benthos, belong the greater part of the diatoms and oscillaria, all murraeocytes and peridinea; further all radiolaria, many globigerina, the hypogenetic medusæ (without alternation of generations), all siphonophores and ctenophores, all chaetognathæ, pteropods, the eopelata, pyrosoma, and thalidæ, etc. Among these we find “purely pelagic, zonary, or bathybic” forms.

The *meroplanktonic* organisms, on the other hand, which are found swimming in the sea only for a part of their life, passing the other part vagrant or sessile in the benthos (either littoral or abyssal), are represented by the following groups: A part of the diatoms and oscillaria, the planktonic *fucoids*, the metagenetic medusæ (*Craspedota* with hydroid nurse, *Aeraspeda* with scyphistoma nurse), some turbellarians and annelids, etc; further, the “pelagic larvae” of hydroids and corals, many helminths and echinoderms, acephala and gasteropods, etc.

## IV.—SUMMARY OF THE PLANKTONIC ORGANISMS.

## A.—PROTOPHYTES OF THE PLANKTON.

The unicellular plants (*Protophyta*\*) have very great importance in the physiology of the plankton and the cycle of matter in the sea (*Stoffwechsel des Meeres*), for they furnish by far the greater part of the fundamental food (*Urnahrung*). The ineneeivable amount of food which the countless myriads of swimming marine animals consume daily is chiefly derived, directly or indirectly, from the planktonic flora, and in this the unicellular protophytes are of much greater importance than the multicellular metaphytes. Nevertheless the natural history of these small plants has thus far been very much neglected. As yet no botanist has attempted to consider the planktonic flora in general, and its relation to the planktonic fauna. Only that single class, so rich in forms, the diatoms, has been thoroughly investigated and systematically worked up; as regards the other groups, not a single attempt at systemization has been made; and many simple forms of great importance have lately been recognized for the first time as unicellular plants. I must, therefore, limit myself here to a brief enumeration of the most important groups of the plankton flora. Its general extent and quantitative development have in my opinion hitherto been much undervalued, and with reference to the cycle of matter in the sea (*Stoffwechsel des Meeres*) deserve a thorough consideration. I find masses of various protophytes everywhere in the plankton, and suspect that they have been negleeted chiefly because of their small size and inconspicuous form. Many of these, indeed, have been regarded as protozoa or as eggs of planktonic metazoa.

As a foundation for a most important province of botany, the classification of the protophytes, we must keep in the foreground the following considerations: (1) The kind of reproduction, whether by simple division (*Schizophyta*) into two, four, or many parts, or by formation of motile swarm-spores, *Mastigophyta*; (2) the constitution of the phytochroms, of yellow, red, or brown pigment, which is distributed in the protoplasm of the cell (usually in the form of granules), and has great significance in assimilation (chlorophyll, diatomin, erythrin, phaeodin, etc.); (3) the morphological and chemical constitution of the cell-membrane (cellulose, siliceous, capsular, or bivalvular, etc.). So long as we hold to the present view of the vegetable physiologists, that for the fundamental process of vegetal assimilation, for the synthesis of protoplasm and amyllum, the presence of the vegetal pigment matter is necessary, we can regard as true protophytes only such unicellular organisms as are provided with such a phytochrom, but we will have to

\*The separation of the *Protophyta* from the *Metaphyta* is as justifiable as that of the *Protozoa* from the *Metazoa*. The latter form tissues, the former do not. (Compare Naturl. Schöpfungsgeschichte, VIII Aufl., 1889, pp. 420-453.)

include here a great number of protista, which have hitherto been reckoned as protozoa, e. g., the *Murraeaceæ*, *Dictyococcæ*, *Peridineæ*. As characteristic and important protophytes of the plankton I here mention seven groups: (1) *Chromaceæ*, (2) *Calcocyceæ*, (3) *Murraeaceæ*, (4) *Diatomeæ*, (5) *Xanthellæ*, (6) *Dictyococcæ*, (7) *Peridineæ*.

1. *Chromaceæ* (30, p. 452).—In this lowest vegetable group is probably to be placed a number of small “unicellular algae” of simplest form, which occur in great abundance in the plankton, but on account of their minute size and simple spherical shape have for the most part been overlooked, or possibly regarded as germ cells of other organisms. They may here be provisionally distinguished as *Procytella primordialis*. The diameter of the spheroidal cells in the smaller forms is only about .001 to .005 mm., in the larger .008 to .012 mm, seldom more. Usually each cell contains only one phytochrom granule of greenish color, sometimes approaching a yellow or red, sometimes a blue or brown. Whether there is also a diminutive nucleus is doubtful. Increase takes place simply by division into two or four parts, and appears to go on with excessive rapidity, but swarm spores do not appear to be formed. Hundreds or thousands of such green spheres may be united in a mass of jelly. The decision whether these simplest *Chromaceæ* belong to the *Chlorococcæ* or *Protoecocæ*, or to some other primitive protophytic group, must be left to the botanist for further investigation, as well as the question whether these diminutive *Procytella* are actually true nucleated cells or only unnucleated cytodes. For our plankton studies these are of interest only so far as they develop in astonishing quantities in many (the colder) regions of the ocean, like the diatoms; and with the latter form a great part of the fundamental food (*Urnahrung*). Over wide areas the sea is often colored brown or green, and they form the chief food (described as *Protoecoccus marinus*) of inconceivable myriads of copepods, as Kükenthal has mentioned in his “Contributions on the Fauna of Spitzbergen.”

2. *Calcocyceæ*.—In the eighth edition of the “*Naturliche Schöpfungsgeschichte*” (30, p. 437) I have designated as *Calcocyceæ* or “unicellular calcareous algae” those important minute organisms which, as “*Coccosphæra*, *Cyathosphæra*, and *Rhabdosphæra*, play a great rôle in oceanic life. They are found abundantly in the plankton of the tropical and subtropical seas, less abundantly in colder zones, and are never absent where pelagic *Thalamophora* occur in great numbers. Like the latter, they are bathypelagic. The ball of protoplasm which completely fills the interior of the small calcareous-shelled plastid seems, when stained red with carmine or brown with iodine, to be unnucleated, and therefore a cytode. The beautiful calcareous plates which compose the shell (*Coccolitha*, *Cyatholitha*, *Rhabdolitha*), and which in the *Rhabdosphæra* bear a radial spine, fall apart after death and are found in great numbers in all parts of the warmer oceans and in the globigerina ooze of the bottom. Murray (5, p. 533; 6, p. 939) and Wyville Thompson (14, I, p. 222)

were the first to demonstrate the wide distribution and innumerable abundance of this unicellular calcareous algæ, and I agree with them in the supposition that these play a significant part in the biology of the ocean and in the formation of its globigerina ooze.

3. *Murraeyteæ*.—Under this name I may here refer to the very important but hitherto neglected group of planktonic protophytes, which were first discovered by John Murray and described under the name *Pyrocystis* (5, p. 533, plate xxi; 6, pp. 935–938). These “unicellular algæ” are transparent vesicles, from 0.5 to 1 or 1.5 millimeters in diameter, and spherical, oval, or spindle-shaped in form. Their simple continuous cell membrane is very thin and fragile, like glass. It is stained blue by iodine and sulphuric acid, and seems to contain a small quantity of siliceous earth. The contents of the vesicle is a vacuolated cell, whose protoplasmic network contains many yellow granules of diatomin. The spherical form (*Pyrocystis noctiluca* Murray) is very similar in size and form to the common *Noctiluca miliaris* and probably is very often mistaken for it. I saw these thirty years ago (1860) at Messina, and later (1866) at Lanzarote, in the Canary Islands.

When John Murray published in 1876 the first figures and careful description, he at first placed them with the diatoms, but later (6, p. 935) he has, with justice, separated them. He there says of *Pyrocystis noctiluca*:

This organism is everywhere present, often in enormous masses, at the surface of the tropical and subtropical oceans, where the temperature is not more than 20° to 21° C., and the specific gravity of the oceanic water is not diminished by the presence of coast and river water. *Pyrocystis* shines very brightly; the light comes from the nucleus and is the chief source of the diffuse phosphorescence of the equatorial oceans in calm weather.

Since these unicellular vegetable organisms do not have the characteristic bivalve shell or siliceous case of the diatoms, but their cell membrane forms a completely closed capsule, they can not be reckoned with the latter, but must be regarded as representatives of a different group of protophytes, for which I propose the name *Murraeyteæ* or “glass bladders” (*Murra*, a name given by the Romans to a glasslike mineral—fluospar (?)—from which costly articles are made).\*

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\*In the Atlantic and Indian oceans I have seen great masses of *Murraeyteæ*, and have distinguished many species, which may be regarded as representatives of four genera: (1) *Pyrocystis noctiluca* Murray; spherical. (2) *Photocystis ellipsoides* Hkl; ellipsoid. (3) *Murraeytis fusiformis* Hkl (*Pyrocystis fusiformis* Murray); spindle-shaped. (4) *Nectocystis murrayana* Hkl; cylindrical. The *Murraeytes* multiply, as it appears, only by simple division (commonly into two parts, less frequently into four). After the nucleus, lying eccentrically or against the cell wall, has divided, there follows division of the soft cell body, which is separated from the firm capsulelike membrane by a wide space (filled with a jelly). Then the membrane bursts, and around the two halves or four tetrads there is immediately formed a new covering. Considered phylogenetically, the *Murraeytes* appear as very old oceanic *Protophytes* of very simple structure. Perhaps they ought to be regarded as the ancestral form of the diatoms, for the bivalvular shell of the latter could have arisen by a simple halving of the capsule of the former.

4. *Diatomeæ*.—The inconceivable quantities in which the diatoms populate the whole ocean and the extraordinary importance which they possess as one of the most important constituents of the “fundamental food supply” (*Urnahrung*) in the cycle of matter in the sea has been considered so many times that it is sufficient here to point to the comparatively recent accounts of Murray (5, p. 533; 6, p. 737, etc.), Fuchs (12, p. 49), Castracane (6, p. 930), and Hensen (9, p. 80). Earlier the chief attention was paid to the benthonic diatoms which everywhere cover the seacoast and the shallow depths of the sea bottom in astonishing quantities; in part fixed on stalks, in part slowly moving among the forests of seaweed and the fixed animal banks (*festsitzenden Thierbanken*) of the coast. The importance of the planktonic diatoms was recognized much later, those abounding in the open ocean as well as in the coast waters furnishing one of the most important sources of food for the pelagic animals. The *oceanic diatoms*, which often cover the surface of the open sea as a thick layer of slime, form another flora, very insufficiently studied and characterized by many forms of colossal size (several millimeters in diameter), peculiarly regular in form, and with extremely thin-walled siliceous shells (species of *Ethmodiscus*, *Coseinodiscus*, *Rhizosolenia*, etc., discovered in such numbers by the *Challenger*). The *neritic diatoms*, on the other hand, which, swimming free in no small numbers, populate the coast waters, are less in diameter and with thicker walls, and stand on the whole between the oceanic and littoral forms. The absolute and relative quantity of the planktonic diatoms seems to increase gradually from the equator towards both poles.

In the tropical zone the pelagic diatoms are much less developed than in the temperate zone, and here again much less than in the polar zone. Wide stretches of the Arctic Ocean are often changed by inconceivable masses of diatoms into a thick dark slime, the “black water,” which forms the feeding-ground of whales. The pteropods and crustaceans, upon which these cetaceans live, feed upon this diatom slime, the “black water” of the Arctic voyager. Not less wonderful are the vast masses of diatoms which fill the Antarctic Ocean south of the fiftieth degree of latitude, and whose siliceous shells, sinking to the bottom after the death of the organism, form the diatom ooze (*Challenger*, stations 152–157). The tow nets here were quickly filled with such masses of diatoms (for the most part composed of *Chatoceros*) that these when dried in the oven formed a thick matted felt (6, p. 920).

5. *Xanthelleæ*.—A highly important share in the cycle of matter in the sea belongs to the remarkable *xanthelleæ* or “yellow cells,” which live in *symbiosis* in the bodies of many marine animals, in the plankton as well as in the benthos. I first proved that these “yellow cells,” which were observed by Huxley (1851) and by Johannes Müller (1858) in the ealymma of radiolarians, were “undoubted cells,” and also described their structure and increase by division (3, p. 84), and later (1870) showed that they constantly contained amylin (4, § 90). But Cien-

kowski first advanced the view that the yellow cells are independent unicellular organisms, parasitic algae, which for a time live in the bodies of the radiolarians, but after the death of the latter come forth and multiply by division. This supposition was confirmed experimentally by Karl Brandt (24, p. 65) and Patrick Geddes, who explained further the nature of their symbiosis, and finally showed the wide distribution of the *xanthellee* in the bodies of numerous marine animals, as well as their production of zoospores (*Zoöxanthella*, *Philozoon*). Whether these are ontogenetically connected with certain "yellow unicellular algae" which live free in the plankton, remains to be farther investigated. Perhaps also in this group belong the *Xanthidea* which were described by Hensen (9, p. 79) and Möbius (10, p. 124) as species of *Xanthidium* and as "spiny cystids," spherical cells which reach 1 millimeter in diameter, contain yellow diatomin granules, and multiply by division. Their thick hyaline shell, which seems to consist of slightly silicified cellulose, armed with simple or star-shaped radial spines, is characteristic. I find these *Xanthidea* very numerous in the oceanic plankton. Perhaps the siliceous-shelled *Xanthidia*, which Ehrenberg has found so abundantly as fossils, also belong here.

6. *Dictyochaæ*.—The ornamented latticed cases of the *Dictyoehidae*, formed of hollow siliceous spicules, are often found in great numbers in the plankton, pelagic as well as zonary. Although these have long been known, both living and as fossils, to microscopists, two very different views as to their true nature are entertained.\*

In a preliminary contribution "On the Structure of *Distephanus (Dictyocha) speculum*" Zoöl. Anzeiger, No. 334, one of my earlier students, Adolf Borgert, briefly showed that each single case contains an independent ciliated cell. He therefore considered it a new group of *Flagellata* (or *Mastigophora*), for which he proposed the term *Silicoflagellata*. The "twin parts" described by me (4, p. 1549) he regarded as a double case which had arisen through the conjugation of two individual *flagellata*. To my mind this new interpretation seems to have very considerable probability, although I do not regard it as settled that the ciliated cells are the swarm-spores of the *Phaeodarium*. In case

\* Ehrenberg, who in 1838 and 1841 first described the ornamented siliceous skeletons of *Dictyocha* and *Mesocena*, called them diatoms and distinguished no less than 50 species of them, some living, some fossil. Later, at Messina (1859), I noticed, inclosed within the ornamented hat-shaped latticed shell a small cell, and on that account referred it to the *Radiolaria*, with reference particularly to the similar siliceous skeletons of some *Nassellaria* (*Acanthodesmida*). Twenty years later R. Hertwig found a spherical *Phaeodarium*, the surface of whose calymma was covered with numerous *Dictyocha* little hats (*Dictyocha-Hütchen*), and he therefore believed that they must belong to this legion. He compares the single siliceous little hats (*Hütchen*) with the scattered spicules of the *Sphaerozoidea*. In my *Challenger* report (4, p. 1558) I agreed with this interpretation; so much the more when I myself saw numerous similar *Phacystina* (*Dictyocha stapedia*) living among a similar *Phaeodaria* in Ceylon, and found specimens in several bottles of the *Challenger* collections, especially from Station 144, from the Cape of Good Hope (4, p. 1561, pl. 101, Figs. 10-12).

the greenish-yellow pigment granules in the protoplasm of the *Dictyochidæ* are chlorophyll or phytochrom, they must be placed with "unicellular algae." If, as I believe, the supposition of Borgert is correct, then the masses of *Dictyochidæ* shells found so abundantly in the calymma of *Phaeodariae* can be regarded only as the empty shells of *Silicoflagellata*, which the skeletonless *Phaeodina* has taken in as food. This supposition is much more probable since these, together with siliceous scales of diatoms and tintinnoids, have been found in great numbers in the calymma of other radiolarians. This case would then be analogous to two similar appearances which I myself have previously described, *Myxobrachia pluteus* (4, p. 22) and *Dalcaromma calcarea* (4, p. 70, § 102).

7. *Peridineæ* (*Dinoflagellata* or *Dinocyea*, earlier *Cilioflagellata*).—This group of *Flagellata* (or *Mastigophora*) earlier placed with the *Infusoria*, has lately, with more certainty, been recognized as a proto-phytic group with vegetable metabolism. They are represented in the plankton by numerous and, in part, remarkable and beautiful forms, a part of which have been lately figured by Stein under the name *Arthrodele flagellata*. Many such forms occur in the neritic, fewer in the oceanic plankton, and often in such masses that they take a great part in the formation of the fundamental food supply. Hensen correctly points out the great importance of these *Protista*, of whose quantity he attempted to give a conception by counting (9; p. 71). Many of these participate in a prominent way in the marine population (*Ceratium*, *Prorocentrum*, etc.). John Murray very often found chains of *Ceratium tripus* (each composed of eight cells) floating in the plankton of the open ocean, without ciliary movements, while the ciliated single cells inhabited the neritic plankton in vast numbers close to the shore. Sometimes these crowds of *Peridineæ*, like the diatoms, appeared so abundantly as to fill the tow net with a yellow slime (6, p. 934).

#### B.—METAPHYTES OF THE PLANKTON.

The only class of metaphytes which occurs in the plankton are the algae. The great majority of this class, so rich in forms, belong to the littoral benthos; only a few forms have adopted the pelagic mode of life, and of these only two, from their great abundance, are of any considerable importance in the oceanic fundamental food supply, the *Oscillatoriæ* which live in the depths, and the *Sargassa* which grow at the surface. A third group, the *Halosphaeræ*, is much less abundant and important, but of considerable interest in many relations.\*

\* The *Oscillatoriæ* must be regarded as true algae, since their characteristic "jointed threads" ("Glieder-fäden") form an actual *Thallus*, and indeed a thread-like thallus, as in the *Conferæ*. But on the same grounds also we must regard as algae the *Volvocineæ* and *Halosphaeræ* with spherical thallus; they are also multicellular *Metaphytes*, which show the simplest form of tissue (*Histoires*, 30, p. 420). The foregoing prototypes, on the other hand, have no tissue, since the entire organism is only a simple cell (*Protista*, 30, p. 453).

1. *Halosphaeræ*.—Under the name *Halosphaera viridis*, Schmitz (1879) first described a new genus of green algae from the Mediterranean, which appear floating in the plankton of the Gulf of Naples in great numbers from the middle of January until the middle of April. They form swimming hollow spheres, from 0.55 to 0.62 mm. in diameter, whose thin cellulose wall is covered within by a single layer of chlorophyll containing cells analogous to the blastoderm of the metazoic egg. Each of these epithelial cells divides later into several daughter cells, each of which forms four cone-shaped swarm-spores with two ciliated cells. I have known this green ball for thirty years. In February, 1860, I found them numerous in the plankton of Messina. I observed a second kind in February, 1867, at Lanzarote, in the Canary Islands. The hollow spheres found in the Atlantic are twice as large, and reach a diameter of 1 to 1.2 mm. They have pear-shaped swarm-spores. I named them *Halosphaera blastula*. Morphologically these hollow spherical algae are of great interest, since they are directly comparable to the blastula (or blastosphere stage) of the metazoic embryo. As the latter is to be regarded as the simplest type of the metazoon, so *Halosphaera* (like *Volvox*) can be looked upon as the primitive ancestral form of the *Metaphyta* (4, p. 499). Hensen has lately found numerous living specimens of *Halosphaera viridis* in five hauls from a depth of 1,000 to 2,000 meters (10, p. 521). The light of the bathybie luminiferous animals may possibly be sufficient for their metabolic activity.

2. *Oscillatoriae*.—Like the diatoms in the cold regions of the ocean, the oscillatoriae (*Trichodesmium* and its allies) are found in the warm regions in inconceivable quantities. It is very certain that the latter, as well as the former, belong to the most important source of the "fundamental food supply." Ehrenberg in 1823 observed in the Red Sea, at Tur, such large quantities of *Trichodesmium erythraeum* that the water along the shore was colored blood-red by them. Möbius has recently carefully described the same thing anew, and has (quite correctly) traced from it the name of the Red Sea (26, p. 7). Later, I myself found just as great numbers as these in the Indian Ocean at Maledira and Ceylon (25, p. 225). In Rabbe's collections are several bottles of plankton (from the Indian and Pacific oceans) entirely filled with them.\* The *Challenger* found great quantities of *Trichodesmium* in the Arafura Sea and Celebes Sea (6, p. 545, 607), and also in the Guinea stream (6, p. 218); and between St. Thomas and the Bermudas (6, p. 136) wide stretches of the sea were colored by it dark red or yellowish brown. Murray found it only in the superficial, never in the deeper layers of the ocean.

3. *Sargassew*.—The higher algae are represented in the planktonic flora only by a single group, the *Sargassew*, and these again are com-

\*In the collection of *Radiolaria*, which may be purchased from the famous Franz Pohle, at Jena, preparation No. 5, from Madagascar, contains many flakes of this *Oscillatoria*.

monly only of a single species, *Sargassum bacchariferum*; but this has the greatest importance, since, as is known, it alone forms the floating sargasso banks, which cover such extensive portions of the ocean. Besides this very important species, other fucoids are found floating in the ocean, especially species of *Fucus* (*F. vesiculosus*, *F. nodosus*, and others). Still they never appear in such masses as the familiar "berry weed." The floating sargasso banks are well known to have their characteristic animal life, which Wyville Thompson accurately described and fittingly termed nomadie (14, II, pp. 9, 339).

This remarkable sargasso fauna bears the same character in both the Atlantic and the Pacific oceans and consists partly of benthonic animals, which live sessile or creeping on the sargasso weed, partly of planktonic organisms which swim among the weeds; the latter are more neritic than oceanic. Hensen has lately described this fauna as remarkably poor, and could only find 10 species of animals in it (9, p. 246). The *Challenger* found more than five times as many species in this same Atlantic sargasso, namely, 55 (6, p. 136). It is obvious that the remarkable negative results of Hensen on this as on other planktonic questions can have no value against the positive results of other investigators.

#### C.—PROTOZOA OF THE PLANKTON.

The two great chief groups of unicellular animals, *Rhizopoda* and *Infusoria*, occur in the ocean in very different proportions, in the reverse condition to that in fresh water.

The *Infusoria* (*Flagellata* and *Ciliata*), which chiefly form the protozoic fauna in the latter, are indeed represented in the sea by a great number of species, but the most belong to the littoral benthos, and only a few swimming species occur in such quantities that they are of importance in the plankton, the *Noctiluceidae* among the *Flagellata*, the *Tintinnoidae* among the *Ciliata*. Much greater is the wealth of the ocean in *Rhizopoda*, calcareous-shelled *Thalamophora* and siliceous-shelled *Radiolaria*. The accumulated masses of these shells form the most important sediment of the ocean, while their unicellular soft bodies constitute the chief food supply for many planktonic animals.

*Infusoria*.—As is known, the *Infusoria* do not play so great a rôle in the life of the ocean as in that of the fresh water. It is true that a great number of *Flagellata* and *Ciliata* occur in the neritic or littoral fauna, but neither on account of the number of individuals nor the richness of forms are they elsewhere of importance, and only a few small groups extend out into the open sea. It seems as if these tender and for the most part uncovered *Protozoa* are not suited for the contest which the wild "struggle for existence" offers here. The armored rhizopods take their place. Still two small and very peculiar groups of *Infusoria* are found in very great numbers in the plankton, and sometimes in such quantities as to form the chief bulk; the *Noctilacea* among

the *Flagellata*, and the *Tintinna* among the *Ciliata*. Both groups, and particularly the *Noctilucidae*, belong to the neritic plankton. They occur in the oceanic only where the coast water flows in (6, pp. 679, 750, 933).

The common *Noctiluca miliaris* and some related species sometimes cover the surface of the coast waters in such masses as to form a thick reddish-yellow slime, often like "tomato soup," and at night are brightly luminous. The *Tintinnoidea* (*Tintinnus*, *Dictyocysta*, *Codonella*) appear in smaller quantities, but often in great numbers. Some forms of these elegant *Ciliata* are oceanic.

*Thalamophora (Foraminifera)*.—The *Thalamophora*, often and very properly called *Foraminifera*, were once generally regarded as benthonic. New observations first showed that a part of these are planktonic, and through the comprehensive series of observations by the *Challenger* the abundant occurrence of these pelagic *Foraminifera* and their great part in the formation of that most important sediment, the *Globigerina* ooze, was first established. All these *Thalamophora* of the plankton belong to the peculiar perforated *Polythalamia*, to the family of the *Globigerinidae*; only *Orbulina* (provided it is independent) to the *Monothalamia*. The number of their genera (8-10) and species (20-25) is relatively small, but the number of individuals is inconceivably great. By far the most important and numerous belong to the genera *Globigerina*, *Orbulina*, and *Pulvinulina*; after these *Sphaeroidina* and *Pullenia*. They occur everywhere in the open ocean in numberless myriads. J. Murray could often from a boat scoop up thick masses of them with a glass, and never fished with the tow net in 200 fathoms without obtaining some (5, p. 534). A few forms (*Hastigerina* and *Cymbalopora*) show more local increase in numbers, while others are rare everywhere (*Chilostomella*, *Candeina*). In the equatorial counter-currents of the Western Pacific, between the equator and the Caroline Islands, the *Challenger* found "great banks of pelagic foraminifera. On one day an unheard-of quantity of *Pulvinulina* was taken in the tow nets; on the following day they were entirely absent, and *Pullenia* was extraordinarily abundant." These important observations by Murray I can confirm from my own experience in the Atlantic and Indian oceans\* (comp. 3, pp. 166, 188).

\* The important relations of these pelagic *Polythalamia* to the rest of the fauna of the plankton on the one side, as well as its importance in the formation of the "*Globigerina* ooze" on the other, has been expressly stated by Murray (6, p. 919). I agree completely with him in the view that these oceanic *Globigerinidae* are true pelagic rhizopods, which in part are found swimming only at the surface or at slight depths (autipelagic), in part at zones of different depths (zonal), but they are not benthonic. The enormous sediment of "*Globigerina* ooze" is composed of the sunken calcareous shells of the dead pelagic animals. On the other hand, the benthonic thalamophores, living partly abyssal, on the bottom of the deep sea, partly littoral, creeping among the forests of seaweed on the coasts, are of other species and genera. They develop a much greater variety of form. The neritic thalamophores found swimming in the coast waters are in part again characterized by various forms.

*Radiolaria*.—No class of organisms has remained so long unknown to us, and by the brilliant discoveries of the last decade has been suddenly placed in so clear a light, as the *Radiolaria* (comp. 4, § 251–260). For half a century we knew next to nothing of these wonderful rhizopods; to-day they appear as one of the most important planktonic classes.\* These, the most varied in form of all the unicellular organisms, form a *purely oceanic class*, and live and swim in all seas, especially in the warmer ones. Numerous species are also found near the coasts, yet these are not distinguishable from those of the open sea. They constitute no separate neritic fauna.

Vast crowds of *Radiolaria* occur at the surface of the ocean, as well as at different depths. Long ago Johannes Müller remarked:

It is a great phenomenon that *Acanthometra* can be taken daily by thousands in a calm sea and independently of storms; and that of many species of *Polycystina*, hundreds of individuals were seen during my last residence at the seashore (2, p. 25).

I have tried myself, on the hundreds of voyages to different coasts which I have made since 1856, to thoroughly study the natural history of the *Radiolaria*. The incomparable collections of the *Challenger* afforded me by far the richest material for observation. The results obtained therefrom are embodied in the report (1887). Among other references to the conditions of the plankton there mentioned, it brought up the following propositions: (1) *Radiolaria* occur abundantly in all seas which contain a medium amount of salt, and which do not (like the Baltic) receive a strong influx of fresh water. (2) In the colder seas only a few species occur (chiefly *Acantharia*), but immense quantities of individuals; towards the equator the variety in form gradually increases (horizontal distribution, comp. 4, § 226–231). (3) The chief groups of *Radiolaria* are distributed unequally in the five bathy-zones or girdles of depth of the open ocean. The subclass *Porulosa* (the two legions of *Spumellaria* and *Acantharia*) inhabit especially the two upper zones. On the other hand, the subclass *Osculosa* (*Nusselaria*

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\*After Ehrenberg, in 1847, had described the siliceous shells of some hundred species from the Barbados, we obtained in 1858 the first description of their organization through Johannes Müller. In the work with which this great master closed his renowned life he described 50 species which he had observed alive in the Mediterranean Sea (2). When in continuation of this I devoted a winter's residence in Messina to their further investigation, I was able in 1862, in the monograph consequent thereupon, to distinguish 144 new species, in all 113 genera and 15 families (3). But this rich *Radiolaria* fauna of Messina still gave no promise of the immense quantities of these delicately ornamented creatures peopling the open ocean, and whose variously formed siliceous shells, sinking to the bottom after death, formed that wonderful sediment, the "*Radiolaria ooze*." This was first discovered thirteen years later by the *Challenger*. The investigation of the fabulous radiolarian treasures (chiefly from the Pacific) which this expedition brought home has led to the discrimination of 20 orders, 85 families, 739 genera, and 4,318 species (4, § 256). Further study of the *Radiolaria* slime of the deep sea will bring to light many new forms from this inexhaustibly rich mine.

and *Phaeodaria*) move in the three lower zones (vertical distribution, 4, § 232-239). The dependence of their appearance upon the various conditions of life has been investigated by Brandt (24, p. 102).

#### D.—COELENTERATES OF THE PLANKTON.

The ancestral group of the coelenterates has important significance and manifold interest for the natural history of the plankton; still this applies in very varied degrees to the different principal groups of this numerous circle (comp. 30, p. 522). The great class of the sponges, which belongs exclusively to the benthos, has never acquired a pelagic habit of life. The phylum of the platodes also needs no further reference here. We know, to be sure, a small number of pelagic turbellarians and trematodes. Arnold Lang, in his monograph on the sea-planarians or polyclads (1884, p. 629), mentions as "purely pelagic" or oceanic 8 species and 4 genera (*Planocera*, *Stylochus*, *Leptoplana*, *Planaria*). Parasitic trematodes are occasionally found as "pelagic parasites" in medusæ, siphonophores, and etenophores; but these trematodes and turbellarians are usually found only individually; they never appear in such quantities as are characteristic of the majority of the plankton animals. Much more important for us is the third type of the coelenterates, the diversified chief group of the nettle animals or *Cnidaria* (30, p. 524).

*Cnidaria*.—With reference to the mode of life and the form conditioned thereby, one may divide the whole group of *Cnidaria* into two great principal divisions, polyps and acalephs, which since the time of Cuvier have lain at the foundation of the older systems. The polyps (in the sense of the older zoologists) embrace all nettle animals, which are fixed to the bottom of the sea, hydropolyps as well as scyphopolyps (*Anthozoa*). They belong exclusively to the benthos. Only a few forms have acquired the pelagic mode of life (*Minyadæ*, *Arachanactis*, larvae of *Actiniæ*, *Cerithiidae*, and some other corals). The second principal division of the nettle animals, the *Acalepha*, embraces, in the sense of their first investigator Eschscholtz (1829), the three classes of medusæ, siphonophores, and etenophores; all swimming marine animals, which, from their richness in forms, their general distribution in the ocean, and their abundant occurrence, possess much importance for plankton study. Since the above-mentioned pelagic polyps (*Minyadæ*, etc.) on the whole are rare, and never appear in great quantities, we need make no further reference to them here. Much more important are the *Acalephs*, which offer a fund of interesting problems for plankton study. Commonly, all these animals are roughly termed "pelagic," but a new consideration shows us that they are so in a very different sense, and that the distinction which we have made above in reference to their chorological terminology here finds its complete justification. We will first consider the medusæ, then the siphonophores and etenophores.

*Medusæ*.—The great interest which I have felt in this wonderful class of animals since my first acquaintance with living medusæ, in 1854, and which has been increased by my numerous sea voyages, led me to the monographing of them (1879). I immediately gained thereby a number of definite chorological and ecological ideas, which have been of permanent influence in the further course of my plankton studies. By it was definitely fixed the knowledge that the whole race of the medusæ is *polyphyletic*, and that on the one side the *Craspedota* (or *Hydromedusæ*) have arisen independently from the *Hydropolyps*, just as on the other side the *Aeraspedota* (or *Seyphomedusæ*) from the *Seyphopolyps*. In both analogous cases the transition to the pelagic, free-swimming mode of life has led to the formation, from a lower, sessile, very simply organized benthic animal, of a much higher planktonic metazoön, with differentiated tissues and organs—a fact which is of great significance for our general understanding of the phylogeny of tissues.

I have in that monograph broadly distinguished two principal forms of ontogeny or individual developmental history among the medusæ, *metagenesis* and *hypogenesis*. Of these I regard metagenesis, the alternation of generations with polyps, as the primary or *palingenetic* form; on the other hand, *hypogenesis*, the “direct development” without alternation of generations, as the secondary abbreviated or *cenogenetic* form. This distinction is of great importance in the chorology, in so far as the great majority of the oceanic medusæ are *hypogenetic*; the neritic, on the other hand, are *metagenic*. To the oceanic medusæ in the widest sense I refer the *Trachylinæ* (*Traehymedusæ* and *Nareomedusæ*) among the *Craspedota*; to the neritic, the *Leptolinæ* (*Anthomedusæ* and *Leptomedusæ*: comp. 29, p. 233). While the former have lost their relation to the benthonic polyps, the latter have retained it through heredity. The same seems to obtain also for the majority of the *Aeraspedota*, namely the *Discomedusæ*. Among these there are only a few oceanic genera with *hypogenesis*, e. g., *Pelagia*. The development of the smaller but very important aeraspedote orders, which I have distinguished as *Stauromedusæ*, *Peromedusæ*, and *Cubomedusæ*, is, I am sorry to say, as yet quite unknown. The first is to be regarded as neritic and metagenic; the two latter, on the other hand, oceanic and hypogenetic. That the majority of the large *Discomedusæ* are neritic and not oceanic is shown from their limited local distribution.

Although ten years ago the *Medusæ* were generally held to be purely pelagic animals, it has now been found that a certain (perhaps considerable) part of them are zonary or bathybic. Among the 18 deep-sea *medusæ* which I have described in part XII of the *Challenger Report* (1881) there are, however, some forms which occur also at the surface, and a few which perhaps were accidentally taken in the tow net while drawing it up. But others are certainly true deep-sea dwellers, as the *Pectyllidæ* among the *Craspedota*, the *Periphyllidæ* and *Atollidæ*.

among the *Aeraspedota*. Some *Medusæ* have partly or entirely given up the swimming mode of life, as *Polyclonia*, *Cephea*, and other *Rhizostoma*, which lie with the back towards the sea bottom, the many-mouthed bunch of tentacles directed upwards. The *Lueernaridae* have completely passed over to the benthos. Many *Medusæ* are spanipelagic, rise to the surface only during a few months (for the purpose of reproduction?), and pass the greater part of the year in the depths; thus in the Mediterranean the beautiful *Cotylorrhiza tuberculata*, *Charybdea marsupialis*, *Tima flavidibris*, and *Olindias müllerii*. These bathybie forms are sometimes brought up in great numbers with the bottom net (19, p. 122). Many cling with their tentacles to *Alyæ* and other objects (20, p. 341).

The immense swarms in which the *Medusæ* sometimes appear, millions crowded thickly together, are known to all seafaring naturalists. Thus in Arctic waters, *Codonium princeps*, *Hippocrene superciliaris*; in the North Sea, *Tiara pileata*, *Aglantha digitalis*; in the Mediterranean, *Liriantha mucronata*, *Rhopalonema velatum*; in the tropics, *Cyanea nigritina*; in the Antarctic Ocean, *Hippocrene nocturna* and others. Hensen (9, p. 65) in the North Sea found a swarm of *Aglantha*, the number of which he estimated at twenty-three and one-half billions. The extent of the multitude was so great that "the thought of approximately estimating the animals in this swarm must be given up." In such cases the whole sea for a few days, or even weeks, seems everywhere full of *Medusæ*; and then again weeks, or even months, may pass without finding an individual. The *uncertainty* of appearance, the "capriciousness of these brilliant beauties," in other words the dependence upon many different, and for the most part unknown causes, is in this interesting animal group remarkably impressed upon us. I will, therefore, in another place, refer to it on the ground of my own experience.

*Siphonophores*.—What I have said above concerning the unequal distribution of the medusæ applies also to their wonderful descendants, the purely *oceanic* class of the siphonophores. This highly interesting class was, up to a few years ago, also regarded as purely pelagic; but of these, too, it is now known that they are in great part bathypelagic, in part also zonary and bathybie. The new and very peculiar group of the *Auronectæ* (*Stephalidæ* and *Rhodalidæ*), taken by the *Challenger* at a depth of 200 to 600 fathoms, is described in my "Report of the Siphonophores of H. M. S. *Challenger*" (1888, p. 296). The *Bathyphysa* taken by Studer, and some of the *Rhizophysidae* (*Aurophysa*, *Linophysa*) captured by the *Gazelle*, were taken at a depth of 600 to 1,600 fathoms (l. c.). But that such deep-sea siphonophores (probably mostly *Rhizophysidae*) inhabited the ocean in great masses was first shown by Chierchia (8, p. 84-86). Previously, in numerous soundings which the *Vettor Pisani* had made in the Atlantic and Pacific oceans, the line of the deep-sea lead when drawn up was found to be wound around with the torn-off stinging tentacles of great siphonophores. By means of

the new closable net invented by Palumbo, he was enabled to bring up the entire animals from definite depths. From these experiments Chierchia concluded "that certain characteristic species of siphonophores live in great numbers at certain depths, from 1,000 meters above the bottom upwards, the strongest and most resistant in the depths, the weaker higher up" (8, p. 86). Other siphonophores, which belong to the forms most numerous at the surface, extend down to considerable depths, as *Diphyes sieboldii* (15, p. 12). The larvae of *Hippopodius luteus*, which are very numerous in winter and spring, have quite disappeared in summer, and, according to Chun, live in greater depths, even to 1,200 meters (15, p. 14). Other forms are spanipelagic and come to the surface only for a short time, only a few weeks in the year, like so many *Physoneectæ*. From these and other grounds the participation of the siphonophores in the plankton, like that of their ancestors, the *Hydro-medusæ*, is extremely irregular, and their appearance at the surface of the sea is subject to the most remarkable changes.

*Ctenophores*.—This *Cnidarian* class also, like the preceding, is purely oceanic, not neritic. They also show the same phenomena of pelagic distribution as the *Siphonophores* and *Medusæ*, frequent appearance in great swarms, sudden disappearance for long periods, unaccountable irregularity in their participation in plankton formation. The tables which Schmidlein has given on the basis of three years' observations, on their periodical appearance in the Gulf of Naples, are very instructive for all three classes of the planktonic *Cnidaria* (19, p. 120). The ctenophores also, up to a short time ago, were regarded as auto-pelagic animals; but of them also it has been discovered that they extend in abundance to various, somewhat definite depths. Chun, in his monograph of the ctenophores of Naples (1880, p. 236–238) has pointed out that these most tender of all pelagic animals have just as definite vertical as horizontal migrations. Many ctenophores, which in the spring are found as larvae at the surface, later sink, pass the summer in the cooler depths, and rise to the surface in the autumn in crowds, as mature animals. The irregularity of their appearance is also mentioned by Graeffe (20, p. 361).

#### E.—HELMINTHS OF THE PLANKTON.

The race of the helminths or "worms" (the cross of suffering for systematic zoölogy) obtains a more natural unity and more logical definition, if one removes therefrom the platodes and annelids, placing the former with the coelenterates, the latter with the articulates. The justice of this limitation and also the grounds for regarding the worms as the common ancestral group of the higher animals, I have set forth already in the "Gastrea Theory" (1873), and many times at later opportunities, last in the eighth edition of my "Natural History of Creation" (1889, p. 540). There remain then as helminths, in the narrower sense, four divisions with about 12 classes, namely, (1) the *Rotatoria*,

(*Trochosphara*, *Ichthydina*, *Rotifera*); (2) the *Strongylariae* (*Nematoda*, *Acanthocephala*, *Chaetognatha*); (3) the *Rhynchocoela* (*Nemertina*, *Enteropneusta*), and (4) the *Prosopygiae* (*Bryozoa*, *Brachiopoda*, *Phoroneae*, *Sipunculae*). The larvae of many of these worms have acquired the pelagic mode of life, but most of them are too small and too scattered in the plankton to be of any considerable importance in its composition.

*Chaetognatha*.—In its mature condition only a single class of helminths plays an independent and indeed an important rôle in the plankton—the small and peculiar class of arrow-worms or *Chaetognatha* (*Sagitta*, *Spadella*, etc.). These, together with the copepods, salpæ, pteropods, and radiolarians belong to the most substantial, most generally distributed, and usually unfailing constituents of the plankton. Hensen (9, p. 59) has made some calculations of the immense numbers in which they appear. He reckons them in the “perennial plankton,” yet does not find “everywhere the regularity which one might expect.” He is astonished at the “highly remarkable variations” in their numbers, and finds this very unequal distribution very puzzling (9, p. 60). Chun has lately shown that the troops of *Sagitta* not only populate the surface of the sea, but also “in common with the *Radiolaria*, *Tomopteridae*, *Diphyidae*, *Crustacea*, constitute the most numerous and most constant inhabitants of the greater depths. In countless multitudes they are taken in the open as well as in the closable net, from 100 meters down to 1,300 meters” (15, p. 17). It seems that *Sagitta*, as a whole purely *oceanic*, is represented by pelagic as well as zonary and bathybie species.

#### F.—MOLLUSKS OF THE PLANKTON.

The race of mollusks play a very important rôle in the plankton. Although the great majority of the genera and species belong to the benthos, yet there are a few families which have become adapted to the pelagic mode of life, of great importance on account of the great swarms in which they often appear. The three chief classes which we distinguish in this race (30, p. 546) live very differently. The *Aecephala*, entirely benthonic, can take part only as swarming larvae in the composition of the plankton; so also the swimming larvae of many meroplanktonic *Gastropoda*. Of these latter only a very few genera have adopted completely the pelagic mode of life, like *Ianthina* among the prosobranchs, *Glaucus* and *Phyllirrhæa* among the opisthobranchs.

*Pteropods and Heteropods*.—These two groups of snails are holoplanktonic, chiefly nyctipelagic animals, which come to the surface of the sea, preferably during the night, in vast numbers (14, pp. 121–125). Chun has lately discovered that many of them are found at considerable depths (15, p. 36). Some kinds of pteropods (e. g., *Spirialis*) seem to belong to the zonary and bathybie fauna. The heteropods are on the whole of less importance. They occur in great swarms less frequently and only in certain parts of the warmer seas. The pteropods on the

other hand surpass the former, not only by a great diversity of genera and species, but particularly from their enormous development in all parts of the ocean. *Clio* and *Limacina* are known to occur in the Arctic and Antarctic ocean in schools so vast as to form the chief food supply of the whales; the swarms of *Creseis*, *Hyalea*, and others which appear in the seas of the warmer and temperate zones, are also so considerable that these fluttering "sea butterflies (*Furfülle di mare*)" often play a very important part in the "cycle of matter in the sea" (*Stoffwechsel des Meeres*). The irregularity of the distribution and phenomena is also shown by the fact that Hensen, during his plankton expedition through the North Sea (July and August, 1887), completely missed the pteropods (9, p. 59; 10, p. 116). On the other hand, when in August, 1879, I fished at Scoury, on the northwest coast of Scotland, we found such immense quantities of *Limacina* (during the forenoon in still weather) that these pteropods certainly formed more than nine-tenths of the entire plankton, and with a bucket we could scoop up many thousands. The mass of the swarm had the same density for a depth of two fathoms and for more than a square kilometer in horizontal extent.

*Cephalopods*.—Although entirely swimming animals, these highly developed mollusks for the most part do not fall under the term plankton, if with Hensen we limit this to those "animals floating involuntarily in the sea" (9, p. 1). They must then be included in the "nekton;" but naturally it depends in some cases entirely on the strength of the current whether the small cephalopods should be included in the former or in the latter. In any case this highest developed class of mollusks is of very great importance in the physiology of the plankton, the question of the "cycle of matter in the sea." On the one hand they daily consume vast masses of pteropods, crustacea, sagitta, medusæ, and other planktonic animals; on the other, they furnish the most important food for fishes and cetaceans. From recent investigations it is found that the cephalopods are partly pelagic, partly zonary or bathybic (*Spirula*, *Nautilus*, etc.). Characteristic small, transparent *Decoleneæ* (*Loligopsidae*) are known as partly pelagic, partly bathybic species (15, p. 36). The same is true also of some *Octoleneæ* (*Philomedidae*). Young forms of cephalopods are captured swimming in the plankton at the surface as well as in the depths.

#### G.—ECHINODERMS OF THE PLANKTON.

The rayed animals in their significance in the plankton, as also in many other morphological and physiological relations, show highly peculiar and varied conditions. Although all echinoderms are without exception purely marine animals, and no single form of this great group inhabits fresh water, still not a single species has completely adopted the planktonic life. Not a single echinoderm in its full-grown and sexually mature condition can be called pelagic. The few forms which temporarily swim about (*Comatulidae*) belong only to the neritic

fauna and do not occur in the ocean. They also are found in such limited numbers that they are without importance for the plankton.

Much more important for us are the free-swimming echinoderm larvæ, which often play a great part in the neritic plankton. Indeed they are classical objects in the history of plankton investigation; for to their study their discoverer, Johannes Müller, forty-five years ago first applied the method of "pelagic fishery with the fine net," which soon led to such remarkable and brilliant results. The distribution and number of the larval rayed animals is naturally dependent upon that of their benthonic parents; but in addition also partly upon chorological, partly æcological causes. According to Sir Wyville Thompson (14, II, pp. 217-245; 6, p. 379), the remarkable metamorphosis, discovered and described in a masterly way by Müller, is the rule only among the littoral forms, chiefly in the temperate and warm zones; on the other hand, it is the exception in the case of the majority, for star animals of the deep sea and cold zones, in the Arctic as well as in the Antarctic, develop directly. Therefore, great troops of pelagic larvæ of these animals occur commonly only in the *neritic plankton* of the temperate and warm zones, not in the open ocean. They seem to visit the depths (below 100 meters) very seldom (15, p. 17). Besides, their appearance is naturally connected with the time of year of this development; often only during a few months (9, p. 62). The variation in the constitution of the "periodic plankton" is here very remarkable.

#### H.—ARTICULATES OF THE PLANKTON.

Of the three chief divisions which we distinguish in the group of articulated animals (30, p. 570) two, the *Annelids* and *Tracheates*, take no part in the constitution of the plankton. Both are represented only by a few pelagic genera, and these have a limited distribution. Much greater in importance is the third chief division, the *Crustacea*. It is the only animal class which is never lacking in the tow-net collections (or only very exceptionally), and which commonly appears in such numbers that their predominant position in the animal world of the sea is evident at the first glance. This applies as well to the oceanic as to the neritic fauna, to the littoral as to the abyssal benthos.

*Annelids*.—The great mass of this group, so rich in forms, belongs to the benthos, and is represented in the abyssal as well as in the littoral fauna by numerous creeping and sessile forms. Only very few ringed animals have acquired the pelagic mode of life and have assumed the characteristic hyaline condition of the oceanic glasslike animals, the swimming *Tomopteridæ* and *Aleiopidae*. Both families are represented in the plankton only by a few genera and species, and as a rule their number of individuals is not very considerable. Chun has lately shown by means of the closable net that both forms, *Tomopteris* as well as *Aleiopis*, are represented in the different depths, from 500 to 1,300 meters, by peculiar zonary and bathybie species, which are distinguishable

from the pelagic species of the surface by characteristic marks. "The wealth in such *Alciopidae* (and *Tomopteridae*) at all depths of 100 meters or over is very surprising, and it requires a careful scrutiny, for the beautiful transparent worms often press actively by dozens in serpentine course through the crowd of other forms in the dishes" (15, p. 24).

*Crustacea*.—In their general œcological importance, in their universal distribution over all parts of the ocean, and especially in their incomprehensible fertility and the abundance of their appearance conditioned thereby, the *Crustacea* surpass all other classes of animals. In the physiology of the plankton the first rank in the animal kingdom belongs to them, as to diatoms in the vegetable kingdom. On the whole, in the organic life of the ocean they have the same predominant importance as the insects for the fauna and flora of the land. In a similar way, as the complicated "struggle for existence" has called up for the latter a quantity of remarkable œcological relations and morphological differences conditioned thereby within the insect class, so has the same occurred in the ocean within the crustacean class. Meanwhile the numerous orders and families of this class, so rich in forms, participate in very different degrees in the constitution of the plankton. The order of copepods by far surpasses all other orders. Next to these follow the ostracods and schizopods, then the phyllopods, amphipods and decapods. The other orders of crustaceans participate in the constitution of the plankton in a much less degree—part of them very little. It is to be added that larvae of all orders may appear in great numbers therein. Thus, for example, the pelagic larvae of the sessile benthonic cirripeds often appear in the neritic plankton so numerously that they constitute four-fifths to nine-tenths or even more of the entire mass.

The chorology of the *Crustacea* offers to the plankton investigator one of the most important and interesting fields of work, the elaboration of which has yet scarcely been begun. The same applies also to the geography and topography of the oceanic and neritic *Crustacea*, both in their horizontal and vertical distribution, to their relations to the benthonic *Crustacea* as well as to the marine fauna and flora in general. As a very important result of the recent discoveries, particularly of the *Challenger*, the fact must here as elsewhere be brought up that in the different groups of *Crustacea* (just as in the *Radiolaria*) the vertical divisions of the planktonic fauna can be very plainly distinguished. Pelagic, zonary, and bathybiic forms are found here in quite definite relations.

*Copepoda*.—As the *Crustacea* are on the whole the most important and influential among the planktonic animals in their œcological relations, so are the copepods among the *Crustacea*. Only one who has seen with his own eyes can gain a conception of the innumerable masses in which these small crustaceans crowd the surface of the ocean as well as the zones of different depths. For days the ship may sail through wide stretches of ocean whose surface always remains covered with the same

yellowish or reddish "animal mush," composed in by far the greater part of copepods. In the journal which I kept in the winter of 1866-67, at Lanzarote, in the Canary Islands, of the varying constitution of the plankton, for many days there is only the remark: "almost pure buckets of copepods," or "the collection consisted almost entirely of *Crustacea*, by far the greater part of copepods." That these small crustaceans form the chief food supply for many of the most important food-fishes (*e.g.*, the herring) has long been known. In the Arctic as well as the Antarctic Ocean *Calanus finmarchicus* and a few related species form in general the chief bulk of the plankton, and furnish food for pteropods and cephalopods, for the divers and penguins, for many fishes and whales. On the voyage from Japan to Honolulu the *Challenger* sailed through wide stretches of the North Pacific Ocean which were covered with red and white patches, caused by great accumulations of two species of small copepods, the red being *Calanus propinquus* (8, p. 758). In many other regions, from the Polar Circle to the Equator, the ship passed through white bands many miles wide, composed solely of copepods (8, p. 843). That their appearance is *very irregular* and dependent on many conditions is true of this very important group of plankton animals as for all others. For two days the *Challenger* went through thick shoals of *Corycaeus pellucidus*. For the next three days the copepods had entirely disappeared.

Hensen has made statistical statements upon the appearance of the copepods of the North and Baltic seas (9, p. 45). Chun has lately shown that this order plays a highly significant rôle, not only at the surface, but also at considerable depths (600 to 1,300 meters), (15, p. 25). "Their abundance and richness in forms in greater depths is absolutely astonishing. Larval forms of species sessile or living upon the bottom mingle in confusion with the young forms and sexually mature stages of epipelagic species. Many species hitherto regarded as varieties are numerously represented in the depths." On the other hand, the order seems to be very poorly represented at very great depths. The *Challenger* found only one very characteristic deep-sea species in 2,200 fathoms—*Pontostratioides abyssicolla* (8, p. 845). Some genera never leave the surface and are autipelagic, *e.g.*, *Pontellina* (15, p. 27).

*Ostracoda*.—The ostracods are, next to the copepods, the most important *Crustacea* of the plankton, and are represented at the surface as well as in different depths by masses of many species. In the zoölogy of the ocean they play a similar rôle, as do the near-related cladocerans (*Daphnidæ*) in the fresh water. The *Challenger* collected 221 species of ostracods. Of these 52 were found below 500 fathoms, 19 below 1,500, and 8 below 2,000 fathoms in depth. Many ostracods, like many copepods and other crustaceans, belong to the most important luminous animals of the ocean. On my journey to Ceylon (in the beginning of November, 1881), as well as on the return trip (middle of March, 1882), I admired as never before the oceanic light in its splendor. "The whole ocean, so far as the eye could reach, was a continuous shimmering sea

of light." Microscopical investigation of the water showed that the luminous animals were for the most part small *Crustacea* (*Ostracoda*), to a less extent *Medusae*, *Salpæ*, worms," etc. (25, pp. 42, 372). Chierchia, three years later, in the same region and in the same month, saw the same brilliant phenomenon: "The most brilliant emerald-green light was produced by an infinitude of ostracods" (8, p. 108).

*Schizopoda*.—Not less important in the planktonic life than the ostracods (sometimes even more important) are the schizopods. They also occur in wide stretches in immense swarms at the surface, as well as in greater and lesser depths. They also play a great rôle in the cycle of matter in the sea (*Stoffwechsel des Meeres*); on the one side since they devour great quantities of protozoa and planktonic larvæ, and on the other because they serve as food for the cephalopods and fishes. Many schizopods, like many ostracods and copepods, belong to the most brilliantly luminous animals, and, like the latter, furnish very interesting problems for the bathygraphy of the plankton. G. O. Sars, who has worked up the rich material collected by the *Challenger*, distinguished 57 species, and found that 32 of these lived only at the surface, 6 from 32 to 300 fathoms, and 4 extended down below 2,000 fathoms (as far as 2,740 fathoms), (6, p. 739). Chun also has discovered in the Mediterranean a number of new zonary and bathybiic schizopods very different from the pelagic varieties of the surface, *Stylochiron*, *Arachnomysis*, etc. (15, p. 30).

The phyllopods (*Daphnidæ*), the amphipods (*Phronimidæ*, *Hyperidæ*), and the decapods (*Miersidae*, *Sergestidae*) are indeed represented in the plankton by a number of interesting forms, partly oceanic, partly neritic; and some of these occasionally appear in considerable quantities. But as a whole they are of far less importance than the copepods, ostracods, and schizopods. The same applies also to the other groups of *Crustacea*, although many of them in their larval state take a great part in the constitution of the plankton. Also in regard to these multiformed and often abundant *pelagic crustacean larvæ*, as well as for the mature crustacean animals, the advancing plankton study has still to establish and explain a fund of facts; namely, in relation to their pelagic, zonary, and bathybiic distribution; their migrations, and the relations in which this planktonic fauna stands to the benthic fauna.

*Insecta*.—That important branch the *Tracheata*, the most numerous in forms of all the principal divisions of the animal kingdom, has in the sea no representatives whatever. The *Protracheata*, *Myriapoda*, and *Arachnidæ* are exclusively inhabitants of the land and in small part of the fresh water, except the pycnogonids or pantopods (in case these really belong to the *Arachnidæ*). Among the *Insecta* there is only a single small group of true marine animals, the family of the *Halobatidae*. These small insects, belonging to the *Hemiptera*, have completely acquired a pelagic mode of life, and run about in the tropical ocean just as our "water-runner" (*Hydrometra*) on the surface of fresh water.

Both of the genera belonging there (*Halobates* and *Halobatodes*, with about a dozen species) are limited to the tropical and subtropical zone. The *Challenger* found them in the Atlantic between 35° north latitude and 20° south latitude; in the Pacific between 37° north latitude and 23° south latitude. I myself observed *Halobates* numerously in the Indian Ocean, and on one day in crowds in the neighborhood of Belligam. Although they can dive, they never go into the depths.

#### J.—TUNICATES OF THE PLANKTON.

The tribe of mantle animals falls into two chief divisions, according to their mode of life. The *ascidians* belong to the *benthos*; all other *tunicates* to the *plankton*. The *Copelata* (or *Appendicularia*) are morphologically the oldest branch of the stem, and are to be regarded as the nearest of the now living relatives of the *Prochordiniae*, the hypothetical common ancestor of the tunicates and vertebrates (30, p. 605). The near relationship of the *Copelata* and the ascidian larva makes it very probable that the whole class of ascidians has sprung from the primarily pelagic *Copelata*, and has diverged from this through the acquirement of a sessile mode of life. The *Lucidiæ* or *Pyrosomidae*, on the other hand, are probably secondarily pelagic animals, and sprang from the *Celocormidae*, a benthonic synascidian group. The *Thalidiae* (the *Doliolidae* as well as the *Salpidae*) are to be regarded as primarily pelagic animals. These conditions are doubly interesting, because the tunicates in an exemplary manner demonstrate the peculiarities which the transition on one side to a sessile mode of life in the *benthos* (in case of the ascidians), and on the other to a free-swimming mode of life in the *plankton* (in the case of all other tunicates), has brought about. All the latter are transparent and luminous fragile animals, poor in genera and species, but rich in numbers of individuals. The ascidians, on the other hand, fastened to the bottom, in part littoral on the coast, in part abyssal in the deep sea, are much richer in genera and species, in many ways adapted to the manifold local conditions of the bottom, and mostly opaque. The few hyaline forms (*e.g.*, *Clarellina*) may be regarded as the remnant of the old ascidian branch, which diverged from the pelagic *Copelata*.

All planktonic tunicates are exquisite *oceanic* animals and all may appear in immense swarms of astonishing extent. Murray (6, pp. 170, 521, 738, etc.) and Chiherchia (8, pp. 32, 53, 75, etc.) met with great swarms of *Appendicularia*, *Pyrosoma*, *Doliolum*, and *Salpa* in the middle of the open ocean, both in the Atlantic and Pacific, particularly in the equatorial zone. I observed the same in the Indian Ocean, between Ceylon and Aden. Further, I have whole bottles full of closely pressed *Thalidiae*, which Captain Rabbe collected in the middle of the Atlantic, Pacific, and Indian oceans, far removed from all coasts. In many log books also these swimming and luminous crowds of *Salpa* and *Pyrosoma* on the open sea, far from all coasts, are spoken of. On the other

hand we know of no *neritic* tunicates, no other forms of swimming mantled animals which are found only on the coasts, except the omnipresent ascidian larva.

Lately Chun has established the interesting fact that the planktonic tunicates occur in numbers not only at the surface and in slight depths, but also during the summer extend down into greater depths (15, pp. 32, 42). He discovered further in the Mediterranean new *Copelata*, which are only zonary or bathybie, never coming to the surface and characterized by peculiar organization as well as difference in size (*Megalocereus abyssorum*, 3 centimeters long, 15, p. 40).

The small, delicate *Copelata* and *Doliola*, from their small size, are naturally more difficult to see than the large luminous *Salpæ* and *Pyrosoma*. Whoever has carefully examined great quantities of oceanic plankton can readily testify that the former also occur almost everywhere and occasionally take an important part in the constitution of the mixed plankton. Among the *Salpæ* there are for example the smaller species which form extensive swimming shoals. From the three-year observations of Schmidtlein it is learned that the salpas belong to the perennial plankton and are numerous throughout the whole year (19, p. 123).

#### K.—VERTEBRATES OF THE PLANKTON.

The vertebrates of the sea are in their mature condition for the most part too large and have too powerful voluntary movements to be reckoned in the true plankton in Hensen's sense, as "animals carried involuntarily with the water." The sea fishes, as well as the aquatic birds and mammals of the sea, overcome more or less easily the impetus of the currents, and thereby prove their independence by voluntary movements, which is not commonly the case with the floating invertebrate animals of the plankton. Meanwhile I have already shown above that this limitation of the *plankton* against the *nekton* is very arbitrary and at any moment may be changed in favor of the latter through diminution of the strength of the current. For the chief point of Hensen's plankton investigation, for the question of the "cycle of matter in the sea," the vertebrates are of greatest importance, since they, the largest of the rapacious animals of the sea, daily consume the greatest quantity of plankton, no matter whether directly or indirectly. A single sea fish of medium size may daily consume hundreds of pteropods and thousands of crustacea, and in case of the giant cetaceans this quantity may be increased ten or a hundred fold. In a comprehensive consideration of the plankton conditions, and particularly in its physiological, ecological, and chorological discussion, a thorough investigation of the vertebrates swimming in the sea, the marine fishes, the aquatic birds, seals, and cetaceans, is not to be undertaken. We can then turn from it here, since it has no further relation to the purpose of this plankton study. We can here in Hensen's sense (9, p. 1)

provisionally limit ourselves to the vertebrates of the sea "carried involuntarily with the water," and as such (apart from a few small pelagic fishes) only the pelagic eggs, young brood, and larvae of the marine fishes come into consideration. Some few teleosts (*Scopelidae*, *Trichiuridae*, *et al.*) occur sometimes in schools in the plankton and are partly autopelagic, partly bathypelagic. The remarkable *Leptcephalidae* are possibly planktonic larvae (of *Muraenoidae*), which never become sexually mature (7, p. 562).

*Fish eggs.*—The planktonic fish eggs, found in great numbers at the surface of the sea, as well as the young fish escaped from them, play without doubt a great rôle in the natural history of the sea. Hensen, whose planktonic investigation started from this point, had thereupon "based the hope to obtain a far more definite conclusion upon the supply of certain species of fishes than had hitherto seemed to be possible" (9, p. 39). But the assumption from which he starts is wholly untenable. Hensen says (*loc. cit.*):

It is scarcely to be doubted that an opinion upon the relative wealth of various kinds of fish in the Baltic or in any other part of the ocean whatever can be obtained through the determination of the quantity of eggs in the area under consideration.

Brandt also characterizes this proposition as very lucid and weighty (23, p. 517).

This standard proposition of Hensen and Brandt, from which a series of very important and complicated computations are to be made, was disposed of in a brilliant manner thirty years ago by Charles Darwin. In the third chapter of his epoch-making "Origin of Species," treating of the "Struggle for Existence," Darwin, under the head of Malthus' theory of population, speaks of the conditions and results of individual increase, the geometric relation of their increase, and the nature of the hindrances to increase. He points out that "*in all cases* the average number of individuals of any species of plant or animal depends only indirectly on the number of seeds or eggs, but directly on the conditions of existence under which they develop." Striking examples of these facts are everywhere at hand, and I myself have mentioned a number of them in my "Natural History of Creation" (30, p. 143). Still, to draw a few examples from the life of the plankton, I recall in this connection many pelagic animals; *e. g.*, crustacea and medusæ. Many small medusæ, which belong to the most numerous animals of the pelagic fauna (*e. g.*, *Obelia* and *Lirope*) produce relatively few eggs; as also copepods, the commonest of all planktonic animals. Incomparably greater is the number of eggs produced by a single large medusa or decapod, which belongs to the rarer species. So, from the number of pelagic fish eggs *not the slightest conclusion* can be drawn as to the number of fish which develop from them and reach maturity. The major portion of the planktonic fish eggs and young are early consumed as food by other animals.

## V.—COMPOSITION OF THE PLANKTON.

The composition of the plankton is in qualitative as well as quantitative relations very irregular, and the distribution of the same in place and time in the ocean also very unequal. These two axioms apply to the oceanic as well as to the neritic plankton. In both these important axioms, which in my opinion must form the starting-point and the foundation for the *ecology and chorology of the plankton*, are embodied the concordant fundamental conceptions of all those naturalists who have hitherto studied carefully for a long time the natural history of the pelagic fauna and flora.

The surprise was general when Prof. Hensen this year advanced an entirely opposite opinion, "that in the ocean the plankton was distributed so equally that from a few hauls a correct estimate could be made of the condition in a very much greater area of the sea" (22, p. 243). He says himself that the plankton expedition of Kiel, directed by him, started on this "*purely theoretical view*," and that it had "*full results* because this hypothesis was proven far more completely than could have been hoped" (22, p. 244).\*

These highly remarkable opinions of Hensen, contradictory to all previous conceptions, demand the most thorough investigation; for if they are true, then all naturalists who many years previously, and in the most extensive compass, have studied the composition and distribution of the plankton are completely in error and have arrived at entirely false conclusions. If, on the other hand, these propositions of Hensen are false, then his entire plankton theory based thereon falls, and all his painstaking computations (on which in the last six years he has spent 17,000 hours, which he wishes to have number the individuals distributed in the plankton) are utterly worthless.

In the first place, the *empirical basis* upon which Hensen founded his assumptions must be proved, "starting from a purely theoretical point of view." The plankton expedition of Kiel was 93 days at sea, and in the months of late summer (July 15 to November 7) which, as is known, offer in the northern hemisphere the most unfavorable time of all for pelagic fishery (28, p. 16, 18). Hensen himself says that it bore the "character of a trial trip" (22, p. 10), and his companion Brandt names it a "reconnaissance" upon which they had come to investigate rapidly

\* Hensen speaks of this in the following terms: "Hitherto it was the prevailing view that the inhabitants of the sea were distributed in schools, and that one, according to luck and chance, according to wind, current, and season, sometimes came upon thick masses, sometimes upon uninhabited parts. This in fact applies only in a certain degree for the harbors. For the open sea our knowledge teaches that normally regular distribution obtains there, which changes in thickness and ingredients only within wide zones corresponding to the climatic conditions. In any case one must seek the variation from such condition according to the cause which has produced it, and the occurrence of inequality is not to be taken as the given starting-point for relative investigation" (22, p. 244).

in succession as great areas as possible" (23, p. 525). In a more remarkable way he adds: "Thereby has resulted the furnishing of a fixed basis for a thorough quantitative and qualitative analysis of marine organisms." According to my view such "fixed basis" was obtained long ago, particularly by the widely extended investigations of the *Challenger* expedition (from January, 1873, to May, 1876), fitted out with all appliances. This embraced a period of forty months, and included "the whole expanse of the ocean." Their experience ought to lay claim to much greater value than that of the *National*, whose voyage of three months took in only a part of the Atlantic, and was in addition trammeled by bad weather, accidents to the ship, early loss of the large vertical nets, and other misfortunes in the carrying out of their plans. It is hardly conceivable how an "exact investigator," from so incomplete and fragmentary experience, can derive the "fixed basis" for new and far-reaching views, which stand in remarkable contradiction to all previous experience.

It would here lead too far, if, from the numerous old and new narratives of voyages, I should collect the observations of seafarers upon the remarkable inequality of the sea population, the different fauna and flora of the regions of currents, the alternation of immense swimming swarms of animals and almost uninhabited areas of sea. It is sufficient to point out the two works in which the most extensive and thorough knowledge up to this time is collected, the "Narrative of the Cruise of H. M. S. *Challenger*," edited by John Murray (6), and the "Collezioni della R. Corvetta Vettore Pisani" (8), published by Chierchia. Since the general chorological and oecological results in these two principal works agree fully with my own views gained from thirty years' experience, I pass immediately to a general exposition of these latter, reserving their proof for a later special work.

#### A.—POLYMICIC AND MONOTONIC PLANKTON.

*The constitution of the plankton of swimming plants and animals of different classes is exceedingly manifold. In this regard I distinguish first two principal forms, polymixic and monotonic plankton.\**

The "mixed tow-stuff (*Auftrieb*), or the *polymixic plankton*," is composed of organisms of different species and classes in such a way that no one form or group of forms composes more than the one-half of the whole volume. The "*simple tow-stuff*, on the other hand, or the *monotonic plankton*," shows a very homogeneous composition, while a single group of organisms, a single species or a single genus, or even a single family or order, forms very predominantly the chief mass of the capture, at least the greater part of the entire volume of the plankton, often two-thirds or three-fourths of it, sometimes even more. Under this monotonic plankton one may again distinguish *preralent plankton*, when the predominant group forms up to three-fourths of the total volume,

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\* Πολύμικτος = much mixed, complex; μονότονος = of a single form, simple.

and *uniform plankton* when this exceeds three-fourths and forms almost the whole mass.

In general the mixed plankton is more abundant than the simple, since as a rule the circumstances of the "struggle for existence" condition and vary in many ways the constitution of the planktonic flora and fauna. Still there are numerous exceptions to this rule, and at many points in the ocean (especially in the zoöcurrents) there occurs locally a development so numerous, and an accumulation of a single form or group of forms in such swarms, that these in the haul of the pelagic net form more than one-half the entire volume. This *monotonic plankton* appears in very different definite forms; for the difference of climate, the season, the oceanic currents, the neritic relation, etc., determine significant differences in the quantitative development of the plankton organisms, which simultaneously appear in vast numbers in a definite region. I will next briefly go over the single forms of the monotonic plankton known to me, passing over, however, the consideration of the extremely manifold composition of the *polymixie plankton*, since I am reserving that as well as a contribution of a number of mixture-tables for a later work.

1. *Monotonic Protophytic Plankton*.—Of the seven groups of pelagic *Protophytes*, at least three, the *Diatoms*, *Murraeaytes*, and *Peridinew*, appear in such quantities in the ocean that they alone may constitute the larger part of the collection of the pelagic nets. The most important and most common is the *monotonic diatom-plankton*, particularly in brackish and coast waters. The siliceous-shelled unicellular *Protophytes* which compose this belong, often predominantly or almost entirely, to a single species or genus, as *Synedre* in the colder, *Chatoceros* in the warmer seas. The colossal masses of Arctic and Antarctic diatoms, which form the "black-water," the feeding-ground of whales, have been mentioned above. In the warmer tropical and subtropical parts of the ocean such accumulations of diatoms seldom or never occur. Here their place is taken by the *monotonic murraeayte-plankton*, composed of immense swarms of nyctipelagic *Pyrocystidae*. Less frequent is the *monotonic peridinea-plankton*. Although these *Dinoflagellata* take a very significant part in the composition, especially of the neritic plankton, yet they do not often occur in such quantities as to form the greater part of the volume of the capture.

2. *Monotonic Metaphytic-Plankton*.—Among the pelagic *Metaphytes* there are only two forms, the *Oscillatoriæ* and the *Sargasseæ*, which appear so numerously that they form the greater part of the pelagic tow-stuff. The *monotonic oscillatoria-plankton*, as a rule formed of swimming bundles of fibers of a single species of *Trichodesmium*, appears in many regions of the tropical ocean in such masses that the quantity of the pelagic fauna is diminished on that account. The *monotonic sargassum-plankton*, formed of "swimming banks" of a single fucoid, *Sargassum baciferum*, is the characteristic massive form of organic life in the *Halistasa* of the "Sargasso Sea."

3. *Monotonic Protozoic-Plankton*.—Among the unicellular *Protozoa*, three different groups, the *Noctiluca*, *Globigerina*, and *Radiolaria*, appear pelagically in such quantities that they form the greater part of the volume of the plankton. The *monotonic noctiluca-plankton* is neritic, and is composed almost exclusively of milliards of the common *Noctiluca miliaris*. It forms the reddish-yellow covering of slime upon the surface of the coast seas, and in the ocean always points out the littoral currents. On the other hand, the widely distributed *monotonic globigerina-plankton* is purely oceanic, the point of origin of the *globigerina* ooze of the deep sea. In different regions of the ocean it is composed of different genera of the above-mentioned pelagic thalamophores. Much more manifold is the *monotonic radiolaria-plankton*, also oceanic. Of these, one can distinguish the three following modifications:\*

(1) *Polycttaria-Plankton*, sometimes composed only of *Collozoum*, sometimes of *Sphaerozoum*, sometimes of *Collosphaera*, most often of a mixture of these three forms; in the warmer seas, partly pelagic, partly zonary; very abundant.

(2) *Acantharia-Plankton*, commonly formed of milliards of a single or of a few species of *Acanthometron* (in the colder seas, e. g., on the east and west coast of South America, south of 40° S. lat.; also north of 50° N. lat. on the coast of Shetland, Faroë-Orkney, and Norway); partly autopelagic, partly bathypelagic.

(3) *Phaeodaria-Plankton*, zonary and bathybic, mostly composed of the larger species of *Aulosphaeridae* and *Sagosphaeridae*, *Calodendridæ* and *Cælographidæ* (e. g., *Cælopégina murrayanum* from the Faroë-Orkney Channel, 4, p. 1757).

4. *Monotonic Cnidaria-Plankton*.—In the group of nettle animals there are numerous forms of medusæ, siphonophores, and etenophores, which appear in immense schools. The *monotone medusa-plankton* is chiefly neritic, composed of very different local forms on the different coasts. Of the larger *Aeraspedota*, in the warmer seas *Rhizostoma* (*Pilemidæ*, *Crambessidæ*) particularly occur; in the colder, *Semostoma* (*Aurelidæ*, *Cyanidæ*), which in schools fill the littoral bays and currents. Of the oceanic *Seyphomedusæ*, *Pelugia* seems to form similar schools. Among the *Craspedota*, monotonic medusa-plankton is especially formed of neritic *Cordonidæ*, *Margelidæ*, and *Eucopidæ*, of oceanic *Æquoridæ*, *Liriopidæ*, and *Trachynemidæ*. *Monotonic siphonophora-plankton* occurs only in the warmer seas, although *Diphyidæ* are found abundantly in all parts of the ocean. The remarkable blue troops of the pelagic *Physalidæ*, *Porpidæ*, and *Vellidæ* have for a long time

\*Radiolarian-plankton is contained in 13 preparations of the Radiolaria collection, which I have collected (1890) and which can be bought through the firm of Franz Pohle at Jena; 8 of these preparations contain polycttaria-plankton, 2 acantharia-plankton, and 3 phaeodaria-plankton. This collection (of 34 microscopic preparations) embraces in addition 17 preparations of the radiolarian-ooze of the deep sea, and 4 preparations of deep sea horny-sponges, whose pseudo-skeleton is composed of radiolarian slime. (Challenger Report, part LXXXII.)

in the tropical and subtropical seas attracted the attention of seafarers by their immense numbers as well as by the irregularity of their sudden appearance and disappearance. Rarer is a purely *physonectic* plankton chiefly composed of *Forskalia*; I have observed such repeatedly at Lanzarote. At that same place also occurred frequently a *monotonic ctenophora-plankton*. These delicate nettle animals also, as is well known, like the *Medusæ* and *Siphonophores*, appear in such closely packed crowds that there is scarcely room between them for other pelagic animals. Not infrequently the great accumulation of a single species of ctenophore imparts to the plankton a very remarkable character, and this is true in all oceans, in the cold as well as in the warm and temperate zones. More often it happens that the monotonic cnidaria-plankton is composed of several species of *Medusæ*, *Siphonophores*, and *Ctenophores*, while other classes of animals take only a very limited share in its constitution.

5. *Monotonic Sagittidae-Plankton*.—The only form of monotonic plankton which the branch of *Helminthes* furnishes is made up by the class of the *Chaetognatha*, various species of the genera *Sagitta* and *Spadella*. Although purely oceanic according to their mode of life, yet they occur numerously in the neritic tow-stuff (*Auftrieb*). Sometimes only a single species of these genera, sometimes several species close together, appear in such swarms as to make up more than half of the entire plankton. These phenomena have been observed in the colder as well as in the warmer seas. In the former the plankton is composed of the smaller, in the latter of the larger species. These forms occur also in the deep sea, and indeed the zonary *sagittidae-plankton* is composed of different species from the pelagic.

6. *Monotonic Pteropoda-Plankton*.—Astonishing masses of oceanic pteropods are very widely distributed in all parts of the ocean, and in part are formed of characteristic genera and species in the different zones. The immense schools of *Clio borealis* and *Limacina arctica*, which inhabit the northern seas and (as "whale-food") furnish the chief food supply for many cetaceans, sea-birds, fishes, and cephalopods, have long been known. But no less immense are other swarms of pteropods, composed of different genera and species, which populate the seas of the temperate and tropical zones. These have often escaped the notice of seafarers, because most species are nyctipelagic. Of the immense quantities of these floating snails, direct evidence is furnished by the accumulated calcareous shells, which in many stretches of ocean (especially in the tropical zone) thickly cover the bottom at depths between 500 and 1,500 fathoms. Often the greater part of this "pteropod-ooze" is formed solely of them (6, pp. 126, 922). At Messina as well as at Lanzarote I found the pteropod-plankton often mixed with considerable numbers of heteropods. Still the latter never form the greater part of the volume.

7. *Monotonic Crustacea-Plankton*.—As the crustaceans surpass all other classes of the animals of the plankton in quantitative development, so they form monotonic plankton far more often than all other classes. Most commonly this simple crustacean-plankton is composed of copepods, not infrequently entirely of a single species (6, pp. 758, 843). Next to this I have more frequently found monotonic *ostracoda-plankton*; next *schizopoda-plankton*. Sometimes also there are in these two orders only numberless individuals of a single species, sometimes of many different species, which compose the monotonic plankton, often almost exclusively, and at other times mixed with additions of other *Crustacea*, *Sagitta*, *Salpa*, etc. The other above-mentioned orders of crustaceans, which also take a considerable part in the constitution of the plankton, the decapods, amphipods, and phyllopods, I have never found in such quantities that they formed more than half of the mass of tow-stuff. On the contrary, such quantities of *crustacean-larvae* of one species (e. g., of *Lepas* and other cirripeds) occasionally appear that they predominantly determine the character of the plankton.

8. *Monotonic Tunicata-Plankton*.—Next to the monotonic forms of plankton, which are composed of *Crustacea* and *Cnidaria*, that of the *Tunicata* is most numerous. Quite preponderant in quantity are the *Thaliidae* or *Salpaceae* (*Salpa* and *Sulphella*), and among these, especially the smaller species (*Salpa democratica-mucronata*, *S. runcinata-fusiformis*, and related species). I have often taken such *monotonic salpa-plankton* in the Mediterranean, in the Atlantic and Indian oceans, and have received the same also through Capt. Rabbe from different parts of the Pacific Ocean. Masses of *Doliolum* and of *Copelata* (*Appendicularia*, *Verrillaria*, etc.) are also commonly mixed with this in greater or less quantities. Still these planktonic tunicates, on account of their small size, recede before the *Salpæ*. I know of no instance where they have by themselves formed a monotonic plankton. But this is the case with the nyctipelagic *pyrosoma*. The *Challenger* and the *Vettor Pisani* in the tropics, on dark nights, met with quantities of *monotonic pyrosoma-plankton* in the middle of the Atlantic and Pacific. By day not a single one of these "cones of fire" was to be seen, and as soon as the moon arose they went into the depths (8, pp. 32, 34).

9. *Monotonic Fish-Plankton*.—If, with Heusen, we limit the term plankton to the *halobios* floating passively in the sea, we can designate as "monotonic fish-plankton" only the schools of very young and small fishes, which often appear abundantly in the currents, occasionally so compact that very few other pelagic animals can find room between them. If one wishes to extend the term still farther, and wipe out the sharp distinction between *plankton* and *nekton*, all those sea fishes (oceanic as well as neritic) which appear in schools, and which play so significant an ecological rôle in the cycle of matter in the sea (e. g., *Scopelidae*, *Clinidae*, *Leptocephalidae*, *Scomberoidæ*) will in general belong here (12, p. 51).

## B.—TEMPORAL PLANKTONIC DIFFERENCES.

The first and most remarkable phenomenon, known to every seafaring planktologist, is the varying constitution of the plankton and the variable mingling of its constituents. The remarkable differences of composition apply *qualitatively* and *quantitatively* to the *oceanic* as well as to the *neritic* plankton. They are just as important in the comparison of different places during the same time as at different times in one and the same place. We can therefore distinguish local and temporal variations, and will first of all consider the latter.

To obtain a complete and more certain survey of the temporary variations of plankton composition, there would be needed especially an unbroken series of observations, which had been carried on at one and the same place at least for the space of a full year—still better for several successive years—to obtain from the yearly and monthly oscillations a general average. Such complete *series of observations*, comparable to the meteorological (with which they stand in direct causal connection), have not hitherto been made. They belong to the most important tasks of the zoölogical stations now everywhere springing up.\*

Meanwhile, a general conception of the considerable size of the yearly and monthly oscillations can be obtained from a comparative summary based upon the important series of observations extending over three years, which Schmidlein has given upon the appearance of the larger pelagic animals in the Gulf of Naples, during 1875–77 (19, p. 120). The contributions of Graeffe upon the occurrence and time of appearance of marine animals in the Gulf of Trieste are also worthy of notice in this connection (20).

The considerable temporal variations which underlie the appearance of the pelagic organisms and which determine such great differences in the plankton composition, relative to quality and quantity, may be divided into four groups: (1) yearly, (2) monthly, (3) weekly, (4) hourly variations. Their causes are manifold, partly meteorological, partly biological. They are comparable to corresponding temporal oscillations of the terrestrial flora and fauna, on one side depending upon climatic conditions and meteorological processes, and on the other upon the changing mode of life, especially upon the conditions of reproduction and development. As the annual development of most terrestrial plants is connected with definite time conditions, as the period of budding and leaf development, of their blossoming and fructification, has

\* My own extensive experience, I am sorry to say, is in this regard very insufficient, since I have never worked at a zoölogical station, and since usually I was only so fortunate as to go to the seacoast for a few months (or even only for a few weeks) during the academic vacation. Only once have I had the opportunity to extend my plankton studies at one and the same place to a half year (from October, 1859, to April, 1860, at Messina, 3, p. v, 166), and three times have I carried them on for three months at the same place—in the summer of 1859 at Naples, in the winter of 1866–67 at Lanzarote, and in the winter of 1881–82 in Ceylon.

become adapted to the meteorological conditions, the time of year and other conditions of life in the "struggle for existence," so also the annual development of most marine animals is governed by definite, inherited habits. With them also the influence of meteorological variations on the one side, of ecological relations on the other, are of the greatest importance for the periodical appearance. Most organisms appear in the plankton only periodically, and only very few can be reckoned as belonging to the "perennial plankton" in Hensen's sense (9, p. 1). This investigator also attaches great importance to the *temporal* "highly remarkable variations" in the plankton composition (9, pp. 29, 59); he explains it in part by "periods of famine" (p. 53).

*Yearly oscillations.*—The plankton literature has hitherto contained only a few reliable statements upon the yearly variations, which underlie the appearance of the pelagic animals and plants. Still there are a few contributions of high merit, extending over a series of years, namely those of Schmidlein from Naples (19) and of Graeffe from Trieste (20). Even the first glance at the tables, those of the former relating to the appearance of the pelagic animals in the Gulf of Naples, shows us how remarkably different was the action of the majority of these in several successive years. As there are good and bad wine and fruit years, so there are rich and barren plankton years. But Schmidlein correctly remarks that extensive observations extending through a long series of years are demanded to gain a deeper insight into the meaning of these yearly and monthly variations shown in the tables. The same view is also held by Chun, who, in his monograph of the ctenophores of the Gulf of Naples (p. 236), points out how very different was the number of these in five successive years.

Graeffe, resting on the basis of his observations for many years, says of *Cotylorhiza tuberculata*, that this beautiful acalyp has not for many years been found in the Adriatic, in other years only individually, but not at all rarely (yet always only in the three months of July, August, and September). Just as variable is the occurrence—"according to the year"—of *Umbrosa lobata* and other medusæ. Of the six species of ctenophores of the Gulf of Trieste, only one appears every year, the five others only now and then. Not only do the *quantities of individuals*, but also the "time of appearance of pelagic animals change according to the meteorological conditions of the time of year" (20, v, p. 361). I myself can fully establish this proposition on the ground of observations which I have made in the course of many years of medusa studies. Many of these "capricious beauties" occur in one and the same place on the Mediterranean coast (*e. g.*, in Portofino, in Villafranca), numerously in the first year, rarely in the second, and not at all in the third. When, in April, 1873, I fished in the Gulf of Smyrna, it was full of swarms of the great pelagic *Chrysaora hyoscella*. In April, 1887, when for the second time I sought the same gulf, I could not find a single individual of that beautiful medusa, but instead the

gulf was filled by crowds of a new, hitherto undescribed, large medusa, *Drymonema cordelia*. Thousands of these *Cyaneidae* lay cast upon the beach at Cordelio.\*

*Monthly oscillations*.—The time of year is of just as great importance for the appearance of very many pelagic animals as for the flowering and fruit formation of land plants. Many of the larger planktonic animals, *Medusae*, *Siphonophores*, *Ctenophores*, *Heteropods*, *Pyrosoma*, etc., appear only in one month or during a few months of the year. They form Hensen's "periodic plankton." In the Mediterranean many pelagic animals are numerous in the winter, while in the summer they are entirely wanting. This "periodical appearance of pelagic animals" has long been known and often mentioned; but not so the important fact that these ethoral periods themselves show considerable variations. For this the tables of Schmidlein (19) and the notes of Graeffe (20) give important points of support. Especially the *Disconectæ* and other *Siphonophores*† behave very irregularly. The cause of the monthly variation lies on the one side in the conditions of reproduction and development; on the other in the varying temperature of the season, as Chun has lately shown (15, 16).

*Daily oscillations*.—Every naturalist who has observed and fished pelagic animals and plants in the sea for a long time, knows how unlike their appearance is on different days in the same period of the year or in the same month, when one may daily hope to find them. As a rule, the weather, and particularly the *wind*, conditions the remarkable difference of appearance. In long-continuing calms the surface of the sea becomes covered with swarms of various pelagic creatures. In long bands, smooth as oil, the most wonderful zoœcurrents appear. But as soon as a fresh wind stirs up lively waves, the majority sink into the quiet depths, and if a more violent storm churns up the deeper layers, all life vanishes from the surface for days. Many animals of the plankton (especially oceanic) are very susceptible to the influence of fresh water, and therefore disappear during violent rains. Warm sunshine entices the one to the surface, while it drives the other into the depths. This influence of the weather upon the quality and quantity of the planktonic composition is so well known that it is not necessary to give examples. Hensen (9) has even gone over his work many times, without thinking how the above endangers his "exact methods" and made their results illusionary.

\* *Drymonema cordelia*, whose milk-white umbrella reaches half a meter in diameter, I will describe hereafter. It differs in the formation of the gonads and oval tentacles, as in several other points, from the Adriatic species, which I have described as *Drymonema victoria* (= *dalmatinum*) (II, 29).

† Of the *Disconectæ* (*Porpita* and *Velella*) Chun during a 7 months' residence at the Canary Islands (1887-88) could find not a single specimen. According to him they should appear first in midsummer (July to September). On the other hand I saw at Lanzarote an isolated swarm of these *Disconectæ* in midwinter, in February, 1867.

*Hourly oscillations.*—Many pelagic animals appear at the surface of the sea *only at a definite hour* of the day, some in the morning, others at noon, still others towards evening. During the remainder of the day not a single individual of the species is to be found. Agassiz, thirty years ago, brought forward noticeable examples of this from the class of *Medusa*, and I can from my own experience adduce a number of other examples. But many other pelagic animals also (*e.g.*, *Siphonophores*, *Heteropods*) come to the surface only for a few hours. We have long known that the swarms of the nyctipelagic *Pteropods*, *Pyrosoma* and many *Crustacea*, come to the surface only during the night and flee the light of day. Other groups act just reversely. But the late extensive observations, especially of Murray (6), Chierchia (8), and Chun (15) have taught us how great is the extent and importance of those hourly variations. That these are of great influence upon the composition of the plankton, and that this accordingly is very different at different times of day, needs no repetition. But we must allude once more to how all these temporal oscillations must be taken into consideration, if the *equality of plankton distribution* is to be proved by observation and estimation. In point of fact they all seem to tend to very remarkable *inequality*.

#### C.—CLIMATIC PLANKTON DIFFERENCES.

The numerous contributions which earlier and later observers have made upon the appearance of the swarms of the pelagic animals in different regions of the ocean, agree in pointing out the differences among them, corresponding to the climatic zones. Thus the Arctic oceans are characterized by masses of monotonic plankton of *Diatom*, *Beroideæ*, *Copepod*, and *Pteropod* groups, swarms which are often composed of milliards of single species. In the oceanic regions of the temperate zone we meet monotonic plankton of the *Fucoid*, *Noctiluca*, *Medusa*, *Ctenophore*, *Salpa*, *Schizopod*, etc., classes, sometimes composed of one, sometimes of several species. In the tropical ocean immense banks of monotonic plankton appear, in which the *Murrayctyes*, *Oscillatoria*, *Physalia*, *Pyrosoma*, *Ostracoda*, determine the character of the swimming oceanic population. Although these facts have long been known, up to this time no attempt has been made to arrange them chorologically or to define more closely the characteristic features of the plankton in the climatic zones. Yet I believe, partly upon the ground of the accounts referred to above (particularly of the *Challenger* and of the *Vettor Pisani*), partly on the ground of my own comparative investigations (of the *Challenger* as well as of the Rabbe collections), that even now an important proposition can be formulated.

*The quantity of the plankton is little dependent upon the climatic differences of the zones, the quality very dependent; especially in this way, that the number of component species diminishes from the equator towards both poles.* This proposition corresponds, on the whole, with the conditions which the climatic differences show in the terrestrial fauna and

flora. Here as there the explanation of the facts is above all to be sought in the influence of the sun, that "all-powerful creator," which in the tropical zone conditions a much more lively interaction of the natural forces than in the polar zones. The "cycle of matter in the sea" (*Stoffwechsel des Meeres*) is no less influenced by the perpendicular rays of the sun than is the terrestrial fauna and flora; and as in the tropics the quantity and the complexity of the terrestrial organic living forms is by far most highly developed, so is it also the case with the marine forms.

Hensen places himself in remarkable opposition to this hitherto accepted view when in his account of the results of the *National* expedition he surprises us with the following statement:

Although we have found plankton everywhere, the amount of it under and near the tropics was relatively small, namely on an average 8 times less than in the north near the Banks of Newfoundland. Each one of these hauls contained upwards of a hundred different forms; but the poverty of the quantity is still a remarkably apparent established fact (22, p. 245).

In the notable account which E. du Bois-Reymond (on January 23, 1890) laid before the Berlin Academy upon the results of the *National* expedition, it was said concerning its scientific results that a complete account could not be given for three years, but then he added:

Only one chief result may here be assumed beforehand. Contrary to all expectations, established upon a theoretical basis, the quantity of plankton in the tropical waters is shown to be surprisingly small (21, p. 87).

Since Hensen with this "chief result" of the *National* expedition stands in strong opposition to the familiar experience of the *Challenger*, of the *Vettor Pisani*, and of many other expeditions, we must first of all again examine the *empirical foundations* upon which his assertions rest. For these he admits that he regards as such only the results of his "trial trip" through a part of the Atlantic ocean, in which the *residence in the tropics* embraced scarcely two months. The results which he here draws from his plankton fisheries, which obviously turned out remarkably poorly as a result of accidental conditions, may contradict the results which were set up by the *Challenger* and the *Vettor Pisani* during a residence in the tropics of altogether four years, in different parts of three great oceans. It is not indeed saying too much, if we declare this kind of conclusion by Hensen as hasty, and the "exact method" which he wishes to establish by *computation* as useless.

My own comparative study of the rich planktonic collections which Murray and Rabbe have brought in from the different parts of the three great oceans, has convinced me that the tropical ocean is not only qualitatively much richer (by the variety and number of planktonic species and genera) than the oceans of the temperate and cold zones, but that it also does not fall behind the latter quantitatively (in the abundant distribution and vast accumulations of individuals). To be sure, one ought not to take into consideration merely the *surface* of the tropical ocean (although this also is often extremely densely populated), but

also the deeper zonary regions. For in the tropical zone there are numerous nyctipelagic organisms, which by day shun the glow of the perpendicular rays of the sun and betake themselves into the cooler, more or less deep layers of water; but at night these bathypelagic animals and plants appear at the surface in such immense crowds that they are not surpassed in quantity by the "immeasurable swarms" of pelagic organisms in the temperate and cold zones.

During my trip through the tropical region of the Indian Ocean, as well on the way to Ceylon (from Bombay) as on the return (from Socotra), I daily wondered at the great richness of pelagic life on the mirrored surface. At night the "whole ocean, as far as the eye could see, was a continuous shimmering sea of light" (25, p. 52). The luminous water, which at night we scooped up directly from the surface with buckets, showed a confused mass of nyctipelagic luminous animals (*Ostracods*, *Salpa*, *Pyrosoma*, *Medusa*, *Pyrocysta*), so closely packed that in a dark night we could plainly read the print in a book by the brightness of their pelagic light. The crowded mass of individuals was not less considerable than I have so often found in the Mediterranean in the currents of Messina. What quantities of food the plankton must here furnish to the larger animals was shown by the vast schools of great medusæ and flying-fish, which for days accompanied our vessel; and this mass covered large areas of the open Indian Ocean, midway between Aden and Ceylon. Just such plankton masses I have received through the kindness of Capt. Rabbe from other tropical parts of the Indian Ocean, between Madagascar and the Cocos Islands, and between these and the Sunda Archipelago. I encountered a wonderfully rich and thick planktonic mass in a pelagic current of the southwest monsoon drift, 50 nautical miles south of Dondra Head, the southern point of Ceylon.\* I have referred to the richness of this in my "Indian Journal" (25, p. 275).

That the *tropical zone of the Atlantic Ocean* also possesses a vast wealth of plankton is shown by many older accounts, but especially from the experience of the *Challenger*. In the middle of the Atlantic, between Cape Verde and Brazil, Murray observed colossal masses of pelagic animals; and if by day they were scarce at the surface, he continually found them below the surface, in depths of 50 to 100 fathoms and more (6, pp. 195, 218, 276, etc.); at night they ascended to the surface and filled the sea far and wide with a brilliant glow (pp. 170, 195, etc.). "On the whole cruise along the Guinea and equatorial currents, the pelagic life was exceedingly rich and varied, in the quantities of individuals as well as of species, much more than anywhere else in the northern or southern part of the Atlantic Ocean. The greatest quantities were seen in the Guinea current during calms, when the sea literally swarmed

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\*A part of the new species of pelagic animals which I found in this astonishingly rich oceanic current are described in my "Reports on the Siphonophora and Radiolaria of H. M. S. *Challenger*."

"with life" (p. 218). This astonishing wealth of plankton was observed in the whole breadth of the Atlantic tropical zone in August and September, 1873; but it was not less than that passed by the *Challenger* on her return in March and April, 1876, in the eastern part of the same region, between Tristan d'Acrenha and Cape Verde. "When the water was calm, an extraordinary superabundance of pelagic life appeared at the surface. *Oscillatoria* covered the sea for miles, and vast quantities of *Radiolaria* (*Collozoum*) filled the nets" (p. 930). With those and other accounts by the *Challenger*, those of the Vettore Pisani quite agree. "*The zone of equatorial calms is out of all proportion rich in organic life.* Sometimes the water seems coagulated, jelly-like, even to the touch. It is impossible to describe the quantities of variously colored forms" (8, p. 31). Chierchia enthusiastically describes the wonderful spectacle which the luminous ocean furnishes at night—"a sea of light which extends to the whole horizon" (pp. 32, 53, etc.). The numerous plankton samples which I myself have investigated from the Atlantic tropical zone show for the most part an extraordinarily rich composition, particularly those between Ascension and the Canary Islands (*Challenger* stations 345 to 353), above all the two equatorial stations 347 and 348, which, like the *Canary currents*, which I studied for three months at Lanzarote, whose fabulous wealth I have already mentioned, also belong to the region of the *tropical trades-drift*.

The quantity and wealth of forms of the plankton in the *tropical zone of the Pacific Ocean* is not less than in the tropical region of the Atlantic and Indian oceans. In the most diverse parts of this region the *Challenger* sailed through "thick banks of pelagic animals." Between the New Hebrides and New Guinea "the surface of the water and its deeper levels swarmed with life. All the common tropical forms were found in great abundance. The list of genera of animals was about the same as in the Atlantic tropical region (pp. 218, 219), but it showed considerable difference in the relative abundance of species" (6, p. 521). Among the Philippines the water showed "a quite uncommon quantity and variety of oceanic surface animals" (p. 662). On the voyage from the Admiralty Islands to Japan the oceanic "fauna and flora of the surface was everywhere especially rich and varied. In the neighborhood of the equatorial countercurrents, between the equator and the Carolines, pelagic foraminifera and mollusks were taken in such quantities in the surface net that they surpassed all earlier observations," etc. (p. 738). On the voyage through the central part of the tropical Pacific, from Honolulu to Tahiti, between 20° N. lat., and 20° S. lat., "the catch of the tow net was everywhere very rich. The superabundance of organic life in the equatorial current and countercurrent is very noticeable, as well with reference to the number of species as of individuals" (p. 776). From this wonderfully rich region, which of all parts of the tropical ocean is farthest removed from all continents, came the absolutely richest plankton samples which I have

ever studied, those which the *Challenger* brought from her stations 262-280. My astonishment was great when I first saw these planktonic masses, in the autumn of 1876; but it grew boundless when a year later I studied preparations taken from them and found in them hundreds of new species of pelagic animals.

The wonderfully rich *Radiolaria* ooze which the *Challenger* brought up at the central Pacific stations 263-274 (from depths of 2,000 to 3,000 fathoms) is only the siliceous remains of that planktonic mass, from which all organic constituents have vanished and the calcareous shells for the most part dissolved by the carbonic acid of the deep currents.\* The numerous surface preparations which Murray finished upon the spot on this remarkable voyage of planktonic discovery through the central Pacific, and mounted in Canada balsam, are *absolutely the richest plankton preparations* which I have ever studied, especially those of stations 266-274, between 11° N. lat. and 7° S. lat. The richest of all stations is 271, lying almost under the equator (0° 33' S. lat., 152° 56' W. long.). I have since shown these preparations for microscopical studies to many colleagues and friends, and they have always expressed the liveliest astonishment over the new "wonder-world" concealed in them. They are jokingly called the "mira-preparations" (comp. 4, §§ 228-235).

The wonderful plankton wealth of the tropical Pacific is as well established by the manifold observations of Chierchia: "*The quantity and quality of the organisms which inhabit the tropical regions of the sea surpass all conception*" (8, p. 75). Inconceivable quantities of pelagic animals of all groups were seen in the middle of the tropical Pacific, between Callao and Hawaii, between Honolulu and Hongkong, not only at the surface, but in the most various depths up to 4,000 meters. The quantity of deep-sea siphonophores was here so enormous that the sounding lead was never drawn up without its being surrounded with torn-off tentacles (p. 85). During the forty days' voyage from Peru to Hawaii the pelagic fishery at the surface as well as in the depths brought to light "such a quantity of different organisms that it must seem almost impossible to one who did not follow the work with his own eyes" (8, p. 88). Similarly, in the Chinese sea and in the Sunda Archipelago immense masses of plankton were encountered.

It is my intention here to bring together the most general impressions of the relative planktonic wealth of the various oceanic regions, which I have gained from a comparative study of many thousand planktonic preparations. The pelagic fauna and flora of the tropical zone is richer in different forms of life than that of the temperate zone, and this again is richer than that of the cold zone of the ocean. This is true of the oceanic as well as of the neritic plankton. Everywhere the neritic plankton is more varied than the oceanic. The wealth of

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\* Of this *Radiolaria* ooze there are 16 samples (embracing about 1,000 different species) contained in the "Radiolarian collection" (1890) above mentioned. The 8 richest of these (Nos. 20-27) belong to the *tropical central Pacific* (stations 265-274).

individuals can in none of these regions be called absolutely greater than in the others, since the quantitative development is very dependent upon local and temporal conditions and, according to time and place, is on the whole extremely irregular. Estimation of individuals can in this relation prove nothing.

#### D.—CURRENTIC PLANKTONIC DIFFERENCES.

By far the most important of all the causes which determine the changing and irregular distribution of the plankton in the sea are the *marine currents*. The fundamental importance of these *currents* for all planktonic studies is generally recognized and has lately been mentioned many times and explained by Murray (6) and Chierchia (8). Even the zoölogists of the plankton expedition of Kiel have not been able to close themselves to this intelligence. Brandt calls special attention to "the importance of the marine currents as a means of, and limit to, the distribution of the planktonic organisms," so that in the various Atlantic currents numerous forms continually appear which were wanting in the regions previously traveled" (23, p. 518). Thus, Hensen mentions the "extraordinarily large plankton catches, which were transported by various currents."

I learned thirty years ago to recognize the great importance of the marine currents and their direct influence upon the composition of the plankton, when at Messina I went out almost daily in the boat for six months to secure the rich pelagic treasures of the strait (3, p. 172). The periodical strong marine current, which there is known to the Messinese under the name of the *current* or the *Rema*, enters the harbor twice daily and brings to it inexhaustible treasures of pelagic animals which since the time of Johannes Müller have aroused the wonder and desire for investigation of all naturalists tarrying there. Not less important did I find later the planktonic importance of the local marine currents (at Lanzarote), when the "Zain" current of the Canary Sea in like manner brought with it an extraordinary wealth of pelagic animals. My companion on the trip, Richard Greeff, has very vividly described these marine currents as "animal roads" (18, p. 307). During my numerous pelagic journeys on the Mediterranean it was always my first care to investigate the conditions of the currents, and on the most different parts of its coast (from Gibraltar to the Bosporus, from Corfu to Rhodos, from Nizza to Tunis, I have always been convinced of the determining influence which they exerted upon the composition and distribution of the plankton.

Although the fundamental importance of the marine currents for the diverse questions of oceanography are now generally recognized, still very little has been done to follow out in detail their significance for planktology. It seems to me, we must here, with reference to our theme, particularly distinguish (1) *halicurrents* (the great oceanic currents); (2) the *bathycurrents* (the manifold deep currents or undercurrents);

(3) the *nerocurrents* (the littoral currents or local coast currents); and  
 (4) the *zoöcurrents* (the local planktonic streams or very crowded animal roads).

*Halicurrents or ocean streams.*—The unequal distribution of plankton in the ocean is in great part the direct result of the oceanic currents. In general the proposition is recognized as true that the great ocean streams, which we briefly designate as *halicurrents*, effect a greater accumulation of swimming organisms and thereby are richer in plankton than the *halistasa* or "still streams," the extensive regions which are inclosed by them and relatively free from currents. For a long time the richness in plankton which characterizes the Gulf Stream on the east coast of North America, the Falkland Stream on the east coast of South America, and the Guinea Stream on the west coast of Central Africa, has been known. Less understood and investigated than these Atlantic streams, but also very rich in varied plankton, are the great streams of the Indian and Pacific oceans, the Monsoon Stream on the south coast of Asia, the Mozambique Stream on the east coast of South Africa, the Black Stream of Japan, the Peru Stream on the west coast of South America, etc.

It is very difficult, from the numerous scattered accounts of the pelagic fauna and flora of these great ocean currents, to form a general picture of them, but it is now possible to draw from them the conclusion that generally the plankton of the *halicurrents*, qualitatively as well as quantitatively, is richer than the plankton of the *halistasa*, or the great oceanic sea basins around which flow the great streams and counter streams, and which meet the first glance on every recent map of the marine currents.\*

In defending this proposition I rely especially upon the rich experience of the two most important plankton expeditions, of the *Challenger* (6) and of the *Vettore Pisani* (8), and also upon my own comparative study of several hundred plankton samples, which were collected in part by Murray, in part by Capt. Rabbe, in the most diverse parts of three great oceans. The planktonic wealth of the great halicurrents is most remarkable at the place where they are narrowest, when the masses of swimming animals and plants are most closely pressed together. Highly remarkable here is the opposition which the rich pelagic fauna and flora of the stream forms in qualitative and quantitative relation to the sparse population of the immediately adjacent halistase. As the temperature and often even the color of the sea

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\* The systematic biological investigation of the *halistasa* seems to me to form one of the nearest and most pressing problems of planktology, and also of oceanography. Apart from the smaller and little investigated Arctic and Antarctic regions, in all five great areas of quiet water ought to be distinguished, namely: (1) the North Atlantic *halistasa* (with the Sargasso Sea); (2) the South Atlantic (between Benguela and Brazil streams); (3) the Indian (between Madagascar and Australia); (4) the North Pacific (between California and China), and (5) the South Pacific *halistasa* (between Chili and Tahiti).

water in two adjacent regions is remarkably different and often sharply contrasted, so also is the constitution of their animal and vegetable world. Thus Murray observed a strong contrast between the cool green coast streams and the warmer deep-blue ocean water when the *Challenger* neared the coast of Chili, between Juan Fernandez and Valparaiso, and correspondingly there occurred a sudden change of pelagic fauna, for the oceanic globigerina disappeared and the neritic diatoms, infusoria, and hydromedusæ appeared in greater abundance (6, p. 833).

This change was very remarkable when the *Challenger* (at station 240, June 21, 1875) left the warm "black stream" of Japan and entered the cold area of quiet water adjacent on the south (about 35° N. lat., 153° E. long.). Great polymixic masses of plankton, dwellers in the first area, were here killed by the sudden change of temperature and replaced by the monotonic copepodan fauna of the cold halistase (16, p. 758). Also, later, on the voyage through the Japan stream, the planktonic contents of the tow net plainly showed the proximity of two different currents. "In the cold streams there appeared a greater mass of small diatoms, noctiluca, and hydromedusæ than in the warmer streams where the richer pelagic animal world (*Radiolaria*, *Globigerina*) remained the same which the *Challenger* observed from the Admiralty Islands to Japan." Many similar cases occurred during the voyage, when proximity to the coast or the presence of coast currents was indicated by the contents of the tow net (6, p. 750).

Observations upon the plankton richness of the oceanic currents, similar to those of Wyville Thompson and Murray on the *Challenger* (6) were made by Palumbo and Chierchia on the *Vettore Pisani*. The latter calls attention especially to the great importance of these and the great accumulation of pelagic animals in limited regions of currents.

It is a fact, that generally on a voyage through the ocean *great quantities of individuals of one species are found pressed together in relatively small spaces*, and this is true of organisms which, on account of their small size, are not capable of extensive movements. In addition, it is also a fact that when the ship is in the midst of the great oceanic currents, the pelagic fishery gives the most brilliant results (8, p. 109). *It is quite certain that the investigation of the distribution of the pelagic organisms can not progress unless accompanied by a parallel study of the currents, the temperature, and the density of the water* (8, pp. 109, 110).

Even the participants in the *National* expedition of Kiel could not avoid noticing the great irregularity of planktonic distribution in the ocean and the importance of the oceanic currents in this respect. During the voyage it was noticed that in different Atlantic currents numerous forms appeared continually which were absent in the regions previously traversed:

The conditions are much more complicated (!) than we had hitherto supposed (23, p. 518).

But it is worthy of notice how Hensen, the leader of this plankton expedition, has noticed this abundant accumulation of pelagic organ-

isms in single regions of currents, and has twisted it in favor of his theory of the *regular distribution of the plankton*:

The tests of the volume of the plankton show that, five times in the north, once north of Ascension, *extraordinarily large catches* (!) were made. These must have been caused by various currents in this region, and can therefore be left *out of consideration* (9, p. 249).

It seems to me that Hensen would have done better to take into consideration these and other facts observed by him relative to the unequal plankton distribution before he built up his fundamental, certainly *adequate*, theory of the equality of the same. This was to be expected, since he himself in his first oceanic plankton studies (1887) observed many "*remarkable inequalities*," and his own tables furnish proof of this. While he many times mentions the immense swarms of *Medusæ* and declares this "quite superabundant accumulation to be mysterious," he adds: "such places must be avoided in this fishery" (9, pp. 27, 65). When Hensen later, in comparing the different catches of copepods (one of the most important planktonic constituents), finds that the distribution of the plankton in the ocean is *very irregular* and that the constitution of this seems to very strongly contradict his general conceptions of natural life (9, p. 52), he holds it to be best that these catches, which are of "such a different kind, should be excluded from consideration" (pp. 51, 53). Also, in the case of *Sagitta*, which Hensen reckons with the copepods as belonging to the uniform perennial plankton, he finds "throughout not the equality which one might expect, but much more remarkable variations" (p. 59).

These "surprising inequalities," "variations even to tenfold," he finds in case of the *Daphnidæ* (pp. 54, 56) and *Hyperidæ* (p. 57), the pelagic larvæ of snails and mussels (pp. 57, 58), *Appendicularia* and *Salpa* (pp. 63, 64), the *Medusæ* and *Ctenophores* (64, 65), the *Tintinnoids* (p. 68), the *Peridiniæ* (p. 71), and even in the *Diatoms* (p. 82)—in brief, in all groups of pelagic organisms which by the numerous production of individuals are of importance for the plankton and upon which Hensen employs his painstaking method of calculation by quantitative planktonic analysis. If one freely "sets apart from consideration" all these cases of remarkable inequality (because they do not fall in with the theoretically preconceived ideas of the equality of planktonic composition), then finally the latter must be proved by counting.

*Bathycurrents or deep streams.*—Through recent investigations, particularly of Englishmen (Carpenter, Wyville Thompson, John Murray, *et al.*), we have become acquainted with the great importance of the submarine currents or deep streams. It has been demonstrated that the *epicurrents*, or the surface streams, furnish us no evidence relative to the undercurrents to be found below them, which we name *bathycurrents*. These undercurrents may in different depths of the ocean have a quite different constitution, direction, and force from the overcurrents. This is as true of the great oceanic as of the local coast currents. If the more accurate study of marine currents is a very difficult

subject and great hindrances lie, as they do, in the way of exact determinations, the same applies especially to the deep currents. New ways and means must first be found for pressing into the dark labyrinth of very complicated physical transactions. Now we can only say that the bathycurrents are of great importance for the *irregular constitution and distribution of the plankton*. Since the time when, through the discoveries of Murray (1875), Chierchia (1885), and Chun (1887), we learned to recognize the existence and importance of the zonary and bathybic fauna, and particularly, through Chun, the *vertical migration* of the bathypelagic animals, the complicated conditions of the submarine currents must evidently have exerted an extraordinary significance for planktology. Although we have hitherto known so little about this subject, yet two points stand out clearly: First, that these are of great influence upon the local and temporal oscillations of planktonic composition; second, that it is an untenable illusion if Hensen and Brandt believe that, by means of their perfect-working vertical plankton net, "a column of water whose height and base area can be accurately determined has been completely filtered" (23, p. 515); for one can never certainly know what considerable changes in the plankton of this column of water one or more undercurrents have caused during the drawing up of the vertical net.

*Nerocurrents or coast streams.*—While the halicurrents or the great ocean streams are influenced in the first place by the winds and stand in immediate connection with the air currents of our atmosphere, it is only partly the case with the local coast currents, for here a number of local causes, which are to be sought in the climatic and geographical condition of the neighboring coast, work together. In the case of coasts which are much indented, in archipelagos with numerous islands, etc., the study of the littoral currents becomes a very complicated problem. The physical and geological natural condition of the coast mountains and of the beach, the number and force of the incoming rivers, the quality and quantity of the coast flora, etc., are here important factors. The fishermen, pilots, etc., are very well acquainted with these local coast currents, which we will briefly call *nerocurrents*, and are usually to be trusted in the details. Scientifically these currents should be studied more closely in smaller part and less quantity. For planktology they are of very high interest and not less important than the oceanic currents.

Next, the above-intimated *reciprocal relations of the neritic and oceanic plankton* are to be taken into consideration. He who for a long time has carried on the pelagic fishery at a definite point on the coast knows how very much the result of this is influenced by the natural condition of the coast, by the course and the extent of the coast currents. Straits like those of Messina and Gibraltar, harbors like those of Villafranca and Portofino, furnish uncommonly rich plankton results, because in consequence of the littoral currents a mass of swimming animals and plants are collected together in a limited space. The vol-

ume of this planktonic mass thus heaped up is often ten or many times greater than that in the immediately adjacent parts of the sea. On the contrary, the planktonic mass is extraordinarily poor in pelagic animals and plants, where by the emptying of great floods a quantity of fresh water is brought into the sea and its saltiness diminished. Johannes Müller pointed out how very much the result of pelagic fishery was influenced thereby. Again, on the other hand, the rivers day by day bring into the sea a quantity of organic substances which serve as food for the benthonic organisms, and since the benthos again stands in manifold reciprocal relation to the plankton, since the meroplanktonic animals (like the medusæ, the pelagic larvae of worms, echinoderms, etc.) are the means of a considerable interchange between the two, so is it easily understood how the distribution of the holoplanktonic animals is also influenced thereby and how irregular becomes the composition of the plankton.

*Zoöcurrents, or planktonic streams.*—Among the most noteworthy and important phenomena of marine biology is the great accumulation of swimming bodies which form long and narrow bands of thickened plankton. All naturalists who have worked at the seashore for a long period and have followed the irregular appearance of the pelagic organisms know these peculiar streams, which the Italian fishermen call by the name “*correnti*.” Carl Vogt, in 1848, pointed out their great importance for pelagic fishery (17, p. 303). For their scientific designation and their distinction from the other marine currents I propose the term *Zoöcurrents* or *Zoörenma*.\*

The pelagic animals and plants are so numerous and so closely packed in these zoöcurrents as to resemble somewhat the human population in the busiest street of a great commercial city. But millions and millions of small creatures from all the above-mentioned groups of planktonic organisms are crowded confusedly together, and furnish a spectacle of whose charm a conception can be formed only by seeing it. If one directly scoops up a portion of this motley crowd with a tumbler, not infrequently “the greater part of the contents of the glass (an actual living animal broth) is composed of the volume of animals, the smaller of the volume of water” (3, p. 171). From a distance these “crowded sea-animal streets” are usually discernible from the smoothness which the surface of the sea presents, while close beside it the surface is more or less rippled. Often one can follow such an “oil-like animal stream,” which usually has a breadth of 5 to 10 meters, for more than a kilometer without finding any diminution of the thick crowd of animals in it, while on both sides of it, right and left, the sea is almost vacant, or shows only a few scattered stragglers. At Messina, as at Lanzarote, the phenomena of the zoöcurrents were especially pronounced. My companion

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\**Rema* (used in Messina) is from the Greek *pevua* = current; comp. 3, p. 172 note.

on the trip, Richard Greeff, has described the Canary animal streams so vividly that I will here give his description verbatim:

Our gaze was directed to the highly peculiar long and narrow currents, which are of very especial importance for pelagic fishery with fine nets. If one looks at the calm sea, especially from an elevation over a wide expanse of water, here and there are seen strongly marked shining streaks, which intersect the surface as long narrow bands. Their course and place of appearance seem to be continually changing and irregular. Sometimes they are numerous, sometimes only few or entirely absent; to-day they appear here, to-morrow there; some have one direction, others the opposite or crossing the first. Occasionally they run along close to one another and unite in a single stream. If one approaches this streak it becomes evident that here in fact a current prevails different from the movements of the surrounding water, and that thereby is brought about the smooth band-like appearance. They give the impression of streams cutting through the rest of the ocean, with their own channel and banks, which, notwithstanding the great variations in the time and place of their appearance, yet during their existence, which is often brief, show a certain independence.

If one comes upon such streams, which are not too far distant from the coast, he sees that all the smaller, lighter objects which formerly scattered over the surface, floated about or east upon the shore, were drawn into it. Pieces of wood and cork, straw, algae, and tangle torn loose from the bottom, all in motley procession are carried along in this current. But in addition (and this is for us the most important phenomenon) all the animals belonging in the region of these currents are drawn in and fill it, often in such great quantities that one is tempted to believe it is not merely the mechanical influence of the narrow stream which has brought about such an accumulation of animals, but that the latter voluntarily seek out these smooth, quiet streams, perhaps in connection with certain vital expressions. A trip upon such a pelagic animal road furnishes a fund of very interesting observations. We can lean over the edge of the boat and review the countless brightly colored sea-dwellers, sometimes passing by singly, so that we can inspect them in their unique peculiarities, sometimes in such thickly massed hordes that they seem to form an unbroken layer of animals for a few feet below the surface. Yet these animal roads, where one meets them in the sea, will always form the most certain and richest mine for the so-called pelagic fauna, although naturally, from their changeableness and their dependence upon a calm sea, they can never be definitely counted upon. Likewise, the origin of these noticeable streams and their significance in the natural history of the sea is still almost completely dark, in spite of the fact that they can be observed in almost all seas and under favorable circumstances daily, and also are known to the fishermen of Arrecife under the name *Zain* (18, p. 307).

Although the zoöcurrents seem to occur in the most diverse parts of the ocean, and have often aroused the astonishment of observers, yet a recent investigation of them is wanting. What I know about them from my own experience and from the contributions of others is essentially the following:

The zoöcurrents occur in the open ocean as well as in the coast regions, particularly in the region of those nerocurrents which run in straits between islands or along indented coasts. They are dependent upon the weather, especially the wind, and appear as a rule only during calms. Although in the case of the neritic zoöcurrents the local course is more or less constant, still it is subject to daily (or even hourly) variations. Their breadth is usually between 5 and 10 meters, but sometimes 20 to 30 meters or more; their length is sometimes only a

few hundred meters, and at others several kilometers. Oceanic animal streams reach much greater extension. Their constitution is sometimes polymixie, sometimes monotonic, often changing from day to day. Highly remarkable is the sharp boundary of the smooth, thickly populated animal roads, especially if the less inhabited and plankton-poor water on both sides is rippled by the wind. What combination of causes produces this vast accumulation is still quite unknown; certainly wind and weather play a rôle in it; often, also, the ebb and flow of the tide and other local conditions of the regions, especially local currents. As whirlwinds on land drive together the scattered masses of dust and smaller objects and raise a column of dust upwards, so may the submarine whirlwind press closely together the bathypelagic planktonic masses and carry them upward to the surface. But probably, also, in the same connection, complicated ecological conditions come into play, *e. g.*, sudden simultaneous development of quantities of eggs of one species of animal. A new study of the zoöcurrents is one of the most urgent problems of planktology.

#### VI.—METHODS OF PLANKTOLOGY.

The new aspects and methods which three years ago were introduced by Prof. Hensen into planktology, and of which I have already spoken, have for their main purpose the *quantitative analysis of the plankton*, *i. e.*, the most exact determination possible of the quantity of organic substance which the swimming organisms of the sea produce. To solve this subject and come nearer to the question connected with it of the "cycle of matter in the sea," Hensen devised a new mathematical method which aims chiefly at the *counting of the individuals of animals and plants* which populate the ocean. This new method we can briefly term the *oceanic population statistics* of Hensen. The high value which this indefatigable physiologist attributes to his new arithmetical method is shown by the special mention which he makes of it in his first contribution (9, pp. 2–33), from the wonderful patience with which he counted for months the single *Diatoms*, *Peridinea*, *Infusoria*, *Crustacea*, and other pelagic individuals in a single haul of the Müller net, and from the long tables of numbers, the numerical protocols, and records of captures which he has appended to his first plankton volume which appeared in 1887.

Any ordinary pelagic haul with the Müller net or tow net brings up thousands of living beings from the sea; under most favorable circumstances hundreds of thousands and millions of individuals.\* How much labor and time was involved in the counting of these organisms (for the greater part microscopic) is shown from the fact that "even the counting of one Baltic Sea catch, which is pretty uniform in its composition, required eight full days, reckoning eight working hours to the

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\* In a small catch, which filtered scarcely 2 cubic meters of Baltic Sea water, were found 5,700,000 organisms, including 5,000,000 microscopic peridinee, 630,000 diatoms, 80,000 copepods and 70,000 other animals (23, p. 516).

day" (23, p. 516). Meanwhile Brandt, explaining the "highly original procedure" of Hensen ("turning attention to attacking a problem, the solution of which no one had ever thought of"), remarks, with reference to the foregoing quantitative analysis of the Atlantic plankton expedition of the *National* (1889), "that the very much more manifold ocean catches will consume presumably twice as much time, and since on the plankton voyage at least 120 such catches were made, then the working out of these (quite apart from the preliminary preparations) will fully occupy an investigator for  $120 \times 14$  days, or about 6 years" (23, p. 516).\*

Opinions respecting the significance and the value of the oceanic population statistics of Hensen are very different. E. du Bois-Reymond, in his paper before the Berlin Academy (21, p. 83),† attributes to it extraordinary importance, "wherefore the uncommon sacrifice made for it was justified." According to his opinion, the plankton expedition of the *National*, arranged for this purpose, within its definite limits, from the novelty and beauty of its well-described task, assumes a unique place, and the Humboldt fund ought to be proud at having been among the first to contribute to its execution" (21, p. 87). On the ground of this honorable recognition, as well as of the great hopes which the naturalist of Kiel himself based upon the results of the *National* expedition, numerous notices have appeared in German newspapers, disseminating the view that an entirely new field of scientific investigation had been thereby actually entered upon, and that a further extension of it was of great importance. I am sorry to say that I can not agree with this very favorable conception.

#### DISTRIBUTION OF THE PLANKTON.

The foundation upon which the entire planktonic conception and computation of Hensen rests is the view "that in the ocean the plankton must be regularly distributed; that from a few catches very safe estimates can be made upon the condition of very great areas of the sea" (22, p. 243). As Hensen himself says, he started with this "*purely theoretical view*," and he believes that a completely successful result is to be had, because these theoretical premises have been more fully

\*According to this, the unfortunate plankton counter would in these 120 catches have to count for over 17,000 hours. How such an arithmetical Danaidæ work can be carried through without ruin of mind and body I can not conceive.

†In the introduction to this noteworthy paper Du Bois-Reymond says that since 1882 Hensen "had been mindful that, especially on the surface of the sea, there was found a more unequally numerous population of minutest living forms than had previously been supposed" (21, p. 83). This remark needs correction, because many times in the celebrated log book of the *National* plankton expedition this has been overlooked, and therefore it has wrongly been inferred that Hensen eight years ago was the first to discover the *existence* and *abundance* of the pelagic fauna and flora. In fact, for forty-five years they have been the object of wonder and study for numerous naturalists.

established than could have been hoped. I have already shown that this fundamental premise is entirely wrong. *The mass of plankton in the ocean is not perennial and constant, but of highly variable and oscillating size.* The biological composition is very diverse, dependent upon temporal variations—year, season, weather, time of day, upon climatic conditions and especially upon the complicated *currentic* conditions of the streams of the sea, of the oceanic and littoral currents, the deep currents, and the local zoöcurrents.

A comprehensive and fair estimation of all these ecological conditions must *a priori* lead to the conviction that *the distribution of the plankton in the ocean must be extremely irregular*, and we find this “purely theoretical view completely established” *a posteriori* by the comparative consideration and comparison of all the earlier above-mentioned observations. These can not be regarded as refuted by the opposing view of Hensen; for the empirical basis of the latter is, in regard to its time and place, *much too scanty and incomplete*.

One might perhaps object that the *technical methods* of plankton capture which Hensen employed gave more complete results than the methods hitherto used; but this is not the case. The recent description which Hensen gives of his technical methods for obtaining plankton (or pelagic fishery) is very praiseworthy (9, pp. 3 to 14). The construction of the net (material, structure of the net, size of filtration), the management of the catch and of the craft, are there carefully described. The advance of the new technique there realized may indeed serve to carry on the pelagic fishery or plankton capture more productively and more completely than was possible with the previous simpler technical apparatus of planktology; but I can not find that one of the proposed improvements of this pelagic technique shows a great advance in principle and is at all comparable to the great advance which Palumbo and Chierchia made in 1884 by the invention of the closable net. Besides, I can not understand how the new “plankton net” constructed by Hensen could give more accurate results than the simple “Müller net” hitherto employed, and the “tow net” used by the *Challenger*. Such a vertical net will always bring up only a part of the plankton contained in the volume of water going through it, and by no means, as Hensen and Brandt believe, is a column of water whose height and base area can be measured with sufficient accuracy *perfectly filtered*. In this supposition the incalculable disturbances by conditions of currents, especially of concealed deep streams, are left out of account, as already mentioned. Besides, Chierchia has lately shown how unreliable and little productive is the fishery with the vertical net on account of the considerable horizontal swimming movements of the pelagic animals (8, p. 79). At any rate, the improvements Hensen has introduced into the technical methods of plankton capture are not so important that the remarkable difference between his and the earlier results can thereby be explained.

## OCEANIC POPULATION—STATISTICS.

Statistics in general is known to be a very dangerous science, because it is commonly employed to find from a number of incomplete observations the approximate average of a great many. Since the results are given in numbers, they arouse the deceptive appearance of mathematical accuracy. This is especially true of the complicated biological and sociological conditions, whose total phenomenon is conditioned by the coöperation of numerous different factors, and is, therefore, very variable according to time and place. Such a highly complicated condition, as I believe I have shown, is the composition of the plankton. If, as Hensen actually wishes, this were to be sufficiently analyzed by counting the individuals, and oceanic population statistics were thereby to be made, then this would only be possible by the formation of numerous statistical tables, which should give results in figures of the plankton fishery quantitatively in at least a hundred different parts of the ocean, and in each of these at least during ten different periods of the year.

A single "reconnoitering voyage" on the ocean, a single "trial trip," limited in time and place, like the three-months Atlantic voyage of the *National* expedition, can furnish only a single contribution to this subject. But it can in no way, as Brandt thinks, offer "firm foundations" for the solution of this and that "thorough analysis" (23, p. 525). If, also, after six years the 120 catches should actually be counted through (after a labor of more than 17,000 hours), if by statistical arrangement of this numerical protocol, by rational reckoning of their results, a serviceable conception of the quantity of individuals of the oceanic region investigated should be obtained, then at best this one computation would give us an *approximate* conception of the conditions of population of a *very small part* of the ocean; but from it by no means can we, as the investigator of Kiel wishes, arrive at conclusions bearing upon the whole ocean; for that purpose hundreds of similar computations must be made, including the most diverse regions and based upon continuous series of observations during whole years. The zoölogical stations would be the best observatories to carry out *complete series of observations* of this character, not such trial trips as the three-months voyage of the *National*.\*

\* In my opinion the results of the *National* expedition of Kiel would have been quite different if it had been carried out in the three months from January to March, instead of from July to October. On the whole, the volume of planktonic catch, at least in the North Atlantic Ocean, would have more than doubled; in some places it would have been increased many fold. Its constitution would have been entirely different. If the expedition had by accident fallen in with a zoöcurrent, and its voyage had continued in it for a few miles, the contents of the nets would have certainly been a hundredfold, possibly a thousandfold, greater.

## COUNTING OF INDIVIDUALS.

Since the new method of oceanic population statistics introduced by Hensen seeks its peculiar basis in the counting of the individuals which compose the plankton, and since it finds in this "counting the only basis upon which a judgment can rest" (9, p. 26), then we must examine more critically this cardinal point of his method, upon which he lays the greatest stress. The counting of the single organic individuals, which compose the mass of the plankton, is in itself, quite apart from its eventual value, an extremely difficult and doubtful task. Hensen himself has not concealed a part of this great difficulty, and attempts to partly allay the doubts which arise against his whole method.\* But in fact these are much greater and more dangerous than he is inclined to admit.

## WHAT IS AN ORGANIC INDIVIDUAL?

This simple question, as is known, is extremely difficult to answer. If one does not accept all the grades of physiological and morphological individuality, which I have distinguished in the third book of my "*Generelle Morphologie*," 1866, there are at least three distinct chief grades to be kept apart: (1) The cell (or plastid); (2) the person (or bud); (3) the cormus (or colony).† Only among the *Protista* (*Protophyta* and *Protozoa*) is the actual individual represented by a single cell; on the other hand, among the *Histona* (*Metaphyta* and *Metazoa*), by

\* The fourth part of the "Methodik" in the plankton volume of Hensen, which treats of "the work on land," (a) Determination of the volume, (b) the counting (9, pp. 15-30), is especially worthy of reading, not only because it gives the deepest insight into the error of his method, but also into his very peculiar conception of a general biological problem.

† The swimming animals and plants which compose the plankton should in this respect be arranged under the following heads: (a) *Protophyta*—among the *Chromaceae*, *Calcoeytiae*, *Murraeytiae*, *Xanthellae*, *Dictyochae*, and *Peridiniae*, all single cells are to be counted; among the diatoms partly the latter, partly the cenobia or cell aggregates. (b) *Metaphyta*—among the *Halosphaera* are to be counted the spherical *Thalli*; among the *Oscillatoriæ* the single, thread-like *Thalli*; among the *Sargasso* the cormus as well as its buds; but the cells which constitute each thallus and bud are also peculiar. (c) *Protozoa*—the *Infusoria* (*Noctiluca* and *Tintinnina*) as well as the rhizopods (*Thalamophora* and *Radiolaria*), are all to be counted as unicellular individuals, but among the *Polycystaria*, besides the *Cenobia* (colonies of *Collozoïde*, *Spharozoïde*, and *Collospheiidæ*). (d) *Cœlenterata*—among the *Medusæ* and *Ctenophores*, as also among the pelagic *Anthozoa* and *Turbellaria* the single persons are to be counted; among the *Siphonophores* these as well as the single colonies; for each person (or each medusom) of a cormus is here equivalent to a medusa. (e) *Tunicata*—among the *Copelata*, *Doliolum*, and the generations of solitary *Salpas*, the single persons are to be counted; on the other hand, among the *Pyrosoma* and the *Salpa* chains, the single cormi as well as the persons which compose them. (f-k) In all the remaining groups of planktonic animals, in the case of sagittæ, mollusks, echinoderm larvae, articulates, and fishes, not merely the persons are to be counted, but also the cells which make up each of these metazoa.

the higher unit of the person or of the colony, which is composed of many cells. If we actually wish to carry out exactly the method, held by Hensen as indispensable, of counting the individuals, and wish to obtain useful results for his statistical work, then nothing remains except a counting of all single cells which live in the sea. For only the single cells, as the "organic elementary individual," can form the natural arithmetical unit of such statistical calculations and the computations based thereon. If Hensen in his long "numerical protocols and comparisons of captures" (9, pp. xi-xxxiii) places close to one another as counted individuals—as coördinated categories—the unicellular radiolaria, the *cormi* of siphonophores and tunicates, the persons of medusæ, ctenophores, echinoderms, and crustacea, the eggs and persons of fishes, then he places together vastly incommensurable bulk of quite different individual value. These can only be comparable for his purpose if all single cells are counted. But since each fish and each whale in the ocean daily destroys milliards of these planktonic organisms, so, in order to gain an "exact" insight into the "cycle of matter in the sea," the cell milliards which compose the bodies of these gigantic animals must be counted and placed in the reckoning.

#### ECONOMIC YIELD OF THE OCEAN.

Hensen holds the quantitative determinations of the plankton not only as of the highest importance in theoretical interest to science, but also in practical interest to national economy. He thinks "that we will be able to invent correct modes of action in the interest of the fisheries,\* only if we are in position to form a judgment upon the productive possibilities of the sea" (9, p. 2). Accordingly he regards it as the most pressing problem to determine the economic yield of the ocean in the same way as the farmer determines the useful yield of his fields and meadows, the yearly production of grass and grain. By the counting of the planktonic individuals which Hensen has carried on for a long time for a small part of the Baltic Sea, he thinks he has become convinced that the "entire production of the Baltic in organic substance is only a little inferior to the yield of grass upon an equally large area of meadow land."

The farmer determines the yield of his meadows, garden, and field by quantity and weight, not by counting the individuals. If instead of this he wished to introduce Hensen's new exact method of deter-

\* How the practical interests of the fisheries can be advanced by quantitative plankton analysis I am not able to understand. The most important modes of action which we can employ for the increase of the fish production of the ocean—artificial propagation, increase and protection of the fry, increase of their food supply, destruction of the predaceous fishes, etc.—are entirely independent of the numerical tables which Hensen's enumeration of individuals gives. That the number of swimming fish eggs furnishes no safe conclusion upon the number of mature fish has been pointed out above.

mination, he must count all the potatoes, kernels of grain, grapes, cherries, etc., and not only that, he must also count the blades of grass of his meadow, even every individual weed which grows among the grain of his field and the useful plants of his garden; for these also, regarded from the physiological point of view, belong to the "total production" of the ground. And what would be gained by all these immense countings? Just as little as with the "desolate figures" in Hensen's long numerical protocols.\*

#### VOLUME AND WEIGHT OF THE PLANKTON.

If one actually regards the determination of the planktonic yield as a highly important subject, and believes that this can be solved by a certain number of quantitative plankton analyses, then this goal can be reached in the simplest way by determination of the volume and weight of each planktonic catch. Hensen himself naturally first trod this nearest way; but he thinks that it is not accurate enough and encounters difficulties (9, p. 15). In his opinion, "an accurate analysis of the plankton, on account of the great variety of its parts, can only be obtained by counting; he quite forgets that such a counting of individuals also possesses only an approximate and relative value, not a complete and absolute one; farther, that from the counting of the different individuals no more certain measure for the economic value of the whole diversely constituted planktonic catch is furnished; finally that the counting of one catch is of highest value as a single factor of a great computation, which is made from thousands of different factors.

The only thorough method of determining the yield, in planktology as in economy, is the determination of the useful substance according to mass and weight and subsequent chemical analysis. In fact, the determination of the planktonic volume, as of the weight, just as the qualitative and quantitative chemical analysis of the plankton, is possible up to a certain degree. The difficulties are less than Hensen believes. It seems odd that the latter has not mentioned these two simplest methods in a single place in his comprehensive volume (9, p. 15), but hastily casts them aside and replaces them with the quite useless "counting of individuals," a Danaidæ task of many years.

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\* While Hensen is going over the counting of the single constituent parts of the plankton, he calls special attention to the fact "that in spite of the apparently" desolate figures, in almost every single case certain results of general interest have come out, though the opportunity is not offered to show them in a comparison.

CYCLE OF MATTER IN THE OCEAN (*Stoffwechsel des Meeres.*)

The many and great questions which the mighty cycle of matter in the ocean furnishes to biology, the questions of the source of the fundamental food supply, of the reciprocal trophic relations of the marine flora and fauna, of the conditions of support of the benthonic and planktonic organisms, etc., have, within the last twenty years, since the beginning of the epoch-making deep-sea investigation (13), been much discussed and have received very different answers (11). Hensen has also devoted considerable attention to this, and particularly emphasizes the physiological importance of the fundamental food supply (*Urnahrung*). He believes this complicated question can be solved especially by *quantitative determination of the fundamental food supply*.

I have already shown why this method of quantitative plankton analysis must be regarded as useless. Even assuming that it were possible and practicable, I can not understand how it could lead to a definite solution of this question. On the other hand, I might here point to one side of the oceanic cycle of matter whose further pursuit seems very profitable. The two chief sources of the "oceanic fundamental food supply" have already been correctly recognized by Möbius (11), Wyville Thompson (13, 14), Murray (6), and others: First, the vast terrigenous masses of organic and particularly vegetable substances, which are daily brought by the rivers to the sea; secondly, the immense quantities of plant food which the marine flora itself furnishes. Of the latter we previously had in mind chiefly the benthonic littoral flora, the mighty forests of algae, meadows of *Zostera*, etc., which grow in the coast waters. Only in recent times have we learned to value the astonishing quantity of vegetable food which the planktonic flora produces, the *Fucoids* of the Sargasso Sea on the one side, the *Oscillatoriae* and the microscopic *Diatoms* and *Peridinea* on the other. But the smaller groups of pelagic *Protophytes*, which I have mentioned above, the *Chromaceae*, *Murrcyceae*, *Xanthelleae*, *Dictyochaeae*, etc., also play an important rôle. The great importance which devolves upon the small symbiotic *Xanthelleae*, has been especially emphasized by Brandt (24), Moseley (7), and Geddes. Evidently their multiplication is extremely rapid, and if each second milliard of such *Protophytes* were eaten by small animals, new milliards would take their places. Whether or not the number of these milliards is shown to us by the quantitative planktonic analysis seems to me wholly indifferent. More important for the understanding of their physiological importance would be the ascertainment of the rapidity of the increase.

The importance of these *Protophytes* and of the *Protozoa* living upon them has lately been particularly described by Chun (28, pp. 10, 13). He has also rightly emphasized the extraordinary importance which the *vertical migration* of the bathypelagic animals has for the support of the deep-sea animals. They are to a great extent the under workmen, who

consstantly bring the provision transports into the deep sea (15, pp. 49, 57). Thither, in addition, come the immense quantities of marine plant and animal corpses, which daily sink into the depths and are borne away by currents. Thither comes the constant "rain" of the corpses of zonary *Protozoa* (especially *Globigerina* and *Radiolaria*), which uninterruptedly pour down through all the zones of depth into the deepest abysses, and whose shells form the most abundant sediment of the deep sea, the calcareous *Globigerina* ooze and the siliceous *Radiolaria* ooze. In general, it seems to me that the daily supply of food materials which the decaying corpses of numberless marine organisms furnish to the others, is much more important than is commonly supposed.\* How much food would a single dead whale alone furnish?

But especially important and not sufficiently valued in this regard, it seems to me, is the trophic importance of the benthos for the plankton. Immense quantities of littoral benthos are daily carried out into the ocean by the currents. Here they soon disappear, since they serve as food for the organisms of the plankton. If one weighs all these complicated reciprocal relations, he obtains without counting a sufficient general conception of the "cycle of the organic material in the marine world."

#### COMPARATIVE AND EXACT METHODS.

The farther the two great branches of biology, namely, morphology and physiology, have developed into higher planes during the last decade, so much farther have the methods of investigation in both sciences diverged from one another. In morphology the high worth of comparative or declarant methods has always been justly more recognized, since the general phenomena of structure (*e. g.*, in ontogeny and systemization) have been in great part removed from exact investigation, and comprise historical problems, the solution of which we can strive for only indirectly (by way of comparative anatomy and phylogenetic speculation). In physiology, on the other hand, we constantly strive to employ the exact or mathematical methods, which have the advantage of relative accuracy and which enable us to trace back the general phenomena of vital activity directly to physical (particularly to chemical) processes. Plainly it must be the endeavor of all sciences (of morphology also) to find and retain as much as possible this exact mode of investigation. But it is to be regretted that among most branches of science (and particularly the biological ones) this is not possible, because the empirical foundations are much too incomplete and

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\* Hensen values this source of food very slightly, because "only a very few animals live upon dead matter," and explains it in this way, "that material in a state of foul putrefaction requires a stronger digestive power than the organization of the lower animals can produce" (9, p. 2). I must contradict both ideas. The sponges live chiefly upon decaying organisms, as do also many *Protozoa*, *Helminths*, *Crustacea*, etc.

the problems in hand much too complicated. Mathematical treatment of these does more harm than good, because it gives a deceptive semblance of accuracy, which in fact is not attainable.\* A part of physiology also embraces such subjects as are with difficulty, or even not at all, accessible to exact definition, and to these also belong the chorology and ecology of the plankton.

The fundamental fault of Hensen's plankton theory in my opinion lies in the fact that he regards a highly complicated problem of biology as a relatively simple one, that he regards its many oscillating parts as proportionally constant bulks, and that he believes that a knowledge of these can be reached by the exact method of mathematical counting and computation. This error is partly excusable from the circumstance that the physiology of to-day, in its one-sided pursuit of exact research, has lost sight of many general problems which are not suited for exact special investigation. This is shown especially in the case of the most important question of our present theory of development, the species problem. The discussions which Hensen gives upon the nature of the species, upon systemization, Darwinism, and the descent theory, in many places in his plankton volume (pp. 19, 41, 73, etc.) are among the most peculiar which the volume contains. They deserve the special attention of the systematist. The "actual species" is for him a physiological conception, while, as is known, all distinction of species has hitherto been reached by morphological means.†

In my Report on the *Radiolaria* of H. M. S. *Challenger* I have attempted to point out how the extremely manifold forms of this most numerous class (739 genera and 4,318 species) are on the one hand distinguished as species by morphological characters, and yet on the other hand may be regarded as modifications of 85 family types, or as descendants of 20 ancestral orders, and these again as derived from one common simple ancestral form (*Aetissa*, 4, § 158). Hensen on the other hand is of the opinion that therein is to be found "a strong opposing proof against the independence of the species" (9, p. 100). He hopes "to lighten the systematic difficulties by the help of computation" (p. 75). Through his systematic plankton investigations he has reached

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\* A familiar and very instructive example of this perverted employment of exact methods in morphology is furnished by the familiar "Mechanical theory of development" of His, which I have examined in my anthropogeny (3d edition, p. 53, 655) as well as in my paper upon *Ziele und Wege der Entwicklungsgeschichte* (Jena, 1875).

† Since of late the physiological importance of the "species" conception has often been emphasized and the "system of the future" by the way of "comparative physiology" has been pointed out, it must here be considered that up to this time not one of these systematic physiologists has given even a hint how this new system of description of species can be practically carried out. What Hensen has said about it (9, pp. 41, 73, 100) is just as worthless as the earlier discussions by Poljáeff, which have been critically considered in my Report on the Deep-Sea Keratosa (*Challenger, Zoölogy*, vol. xxxii, part 82, pp. 82-85.)

the conviction that "the more accurately the investigation has been made, so much the more plain becomes the distinction of species" (9, p. 100). On the other side I, like Charles Darwin, through many years of comparative and systematic work, have arrived at the opposite conclusion: "*The more accurately the systematic investigations are made, the greater the number of individuals of a species compared, the intenser the study of individual variation, by so much more impossible becomes the distinction of actual species, so much more arbitrary the subjective limits of their extent, so much stronger the conviction of the truth of the Theory of Descent.*"\*

#### PLANKTOLOGICAL PROBLEMS.

The wonderful world of organic life, which fills the vast oceans, offers a fund of very interesting subjects. Without question, it is one of the most attractive and profitable fields of biology. If we consider that the greater part of this field has been open to us scarcely fifty years, and if we wonder at the new discoveries which the *Challenger* expedition alone has brought to light, then we ought to count upon a brilliant future for planktology.

Above all we ought to cherish the hope that our German *National* expedition, the first great German undertaking in the field, may promote many planktonic problems, and that the six naturalists who, under such favorable conditions and with such important instruments, studied the oceanic plankton for ninety-three days and in 400 hauls of the net were able to obtain a rich collection of pelagic organisms, will by their careful working up of these enrich our knowledge many fold. However, the preliminary contributions of Hensen (22) and Brandt (23) give us no means of passing judgment upon the matter now. Among the results which the former has briefly given to the Berlin Academy few require consideration; but for this the difference of our general point of view is to blame. Thus, for example, I have attempted to explain the remarkable "similarity to water of the pelagic fauna," the transparency of the colorless glassy animals, in 1866, in my General Morphology (II, p. 242), according to Darwin's Theory of Selection, by natural selection of like colors (30, p. 248). Hensen, on the other hand,

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\* F. Heineke has briefly, in his careful "Investigations upon the Stickleback," given expression to the same conviction in the following words: "All the conclusions here deduced by me are simply and solely founded upon the comparison of very many individuals of living species, or, in other words, upon the study of *individual variation*. I am convinced that in essentials the study of embryology will confirm my theory. It will be a proof of this, that he who wishes accurately to describe related species, and races of a species, and to study their genealogical relation to one another, must begin by comparing a very great number of individuals from different localities accurately and methodically. He will then soon see that proofs of the theory of descent by this means are found in great numbers at all times, if only one does not spare the pains to trace them out." (Oversigt af K. V. Akad. Forh. Stockholm, 1889, No. 6, p. 410.) This view of Heineke is shared by every experienced and unbiased systematist.

regards hunger as the cause of this, and the "tendency to explore a relatively great bulk of water." In general, according to his view, "many larger pelagic animals bear the outspoken character of unfavorable conditions of life, of a life of hunger."

Regarding the *appearance* of many pelagic animals *in swarms*, Hensen explains "that the young do not float, but swim freely. In consequence of this, the mother animals drive them away, and if the larvae finally rise to the surface the former can not enter into competition with them" (22, p. 252). The accumulation of numbers of *Physalia* in great swarms stands, according to his view, in correlation with the mode of movement. The animals which are capable of no independent movement of progression must remain rather closely crowded together, in order to be able to reproduce *bisexually*; those carried too far away must perish." On the other hand it is to be noted that the *Physalia* is not, as Hensen assumes, *gonochoristic*, but always *hermaphroditic*.\*

The above-mentioned phenomena, the similarity to water of the pelagic fauna, the periodic appearance of many pelagic organisms in swarms, their abundant accumulation in the zoocurrents (p. 85), particularly their relation to the currents, are only a few of the greater problems which planktology furnishes for human investigative energy. For these, as for so many other fields of biology, Charles Darwin, by the establishment of the descent theory, has opened to us the way to a knowledge of causes. We must study the complicated reciprocal relations of the organisms crowded together in the struggle for existence, the interaction of heredity and variation, in order to learn to understand the life of the plankton. But in these plankton studies, as well in physiological as in morphological questions, we must use that method which Johannes Müller, the discoverer of this field, always employed in a manner worthy of imitation: simultaneous "observation and reflection."

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\* The cormi of all *Physalidae* are monoecious, their cormidia monoclinic. Each single branch of the racemose gonodendron is monostylie, and bears one female and several male medusoids. The facts were brought out thirty-five years ago by Huxley. (Compare my Report on the Siphonophore: Zoölogy of the *Challenger*, vol. xxviii, pp. 347, 356.)

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