THE IMPORTANCE OF UPWELLING WATER TO VERTEBRATE PALEONTOLOGY AND OIL GEOLOGY

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INTRODUCTION.

This study originates from a visit to the beach of Walvis Bay (S W Africa) on November 24th, 1938. A mass mortality of fish had taken place some days before and fishes were scattered all over the beach. In this region such a mass mortality occurs every year in the southern summer. As a result the sediment of the bay itself and of a great area of the open sea outside it contains innumerable fish remains; moreover, the sediment shows various other peculiarities, that will be described below. The peculiarities of the sediment reminded me of bituminous fish shales; the similarity being particularly striking with those shales that consist for a considerable part of the siliceous material of fossil diatoms (Californian Monterey shales, menelite shales of the Carpathians, etc.).

A further peculiarity of the Walvis Bay region is the rainlessness. This reminded me of the fact that bituminous shales often show some association with terrestrial sediments testifying of a very dry climate. To ascertain the causes of these similarities firstly I searched for the cause of the mortality, which until now has not been convincingly elucidated. The cause of this mortality as well as the cause of the peculiarities of the sediment and of the rainlessness of the coast region are discussed in the present paper (cf. preliminary papers, BRONGERSMA, 1943, 1944, 1945, 1947*b*); the similarity with the above mentioned shales will be treated of in a separate paper.

CHAPTER I.

Description of the sediment of the azoic zone near Walvis Bay.

The seafloor deposits along the coast of Southwest Africa, especially between latitudes 21° 30′ S and 24° 30′ S, have a very unpleasant odour reminiscent of H_2S and of the odour characteristic of putrefaction. This area stretches nearly from Cape Cross to south of Conception Bay, a distance of approximately 200 miles and from the coast line 25—30 miles west. In the years 1925—1927 this area was studied by the Fisheries and Marine Biological Survey of the Union of South Africa (VON BONDE, 1928*a*, p. 12; idem, 1928*b*, p. 18; MARCHAND, 1928). The bottom samples obtained within this area were in almost all cases alike, being composed of soft, dark green mud smelling of H_2S. Bottom living invertebrates are very scarce in this region. Bottom feeding fish are scarce too. On account of the scarcity of bottom living organisms the area is called the "azoic zone". At the latitude of Walvis Bay the azoic zone stretches to a maximum depth of 77 fathoms and at the latitude of Conception Bay to about the 84 fathom line. "Immediately the 84 fathom line is left behind, the bottom although still composed of green mud, becomes firmer in consistency, and there is a marked absence of the sulphurous smell." (VON BONDE, 1928*b*, p. 20).

Within the area extending from Pelican Point to 23° 38′ S, there is a narrow belt between the azoic zone and the shore where the bottom consists of fine grey sand, and the absence of green sulphurous mud is noteworthy (see fig. 1); here living marine fauna and flora abound.

A chemical and biological analysis of the sediment of the azoic zone is given by COPENHAGEN (1934). Bottom samples collected in this zone by the Meteor expedition are described by PRATJE (1935, p. 50). According to COPENHAGEN the green mud contains a quantity of H_2S varying from 44 cm^3 to 79 cm^3 of gas (apparently in 100 cm^3 of sediment) at NTP. The lower H_2S content was found in a sample collected close inshore, and containing an appreciable quantity of sand particles. Within the sediment life is possible only for anaerobic bacteria; sulphate reducing bacteria are abundant. The sediment is devoid of living aerobic organisms, plants as well as animals. Dead remains of some groups of aerobic organisms, however, are numerous. The sediment consists for a very considerable part (60 % dry weight) of the siliceous skeletons of diatoms. According to PRATJE (1939, p. 1669) it is a true diatom ooze. Further, fish remains may be brought up by the bucketful. Remains of invertebrates are very scarce. As the outer limit of the azoic zone is approached the percentage of diatomic skeletons decreases greatly, while tests of foraminifera increase greatly in number. Numerous empty shells of the mollusk *Crassatella* *africana* are found near the westward edge of the azoic zone. Outside this region, where the bottom samples have no smell of H_2S any more, live specimens of this mollusk are brought up commonly in the trawl, while other evidences of marine fauna, such as worms, crustaceans, holothurians, etc., are numerous too (MARCHAND, 1928).

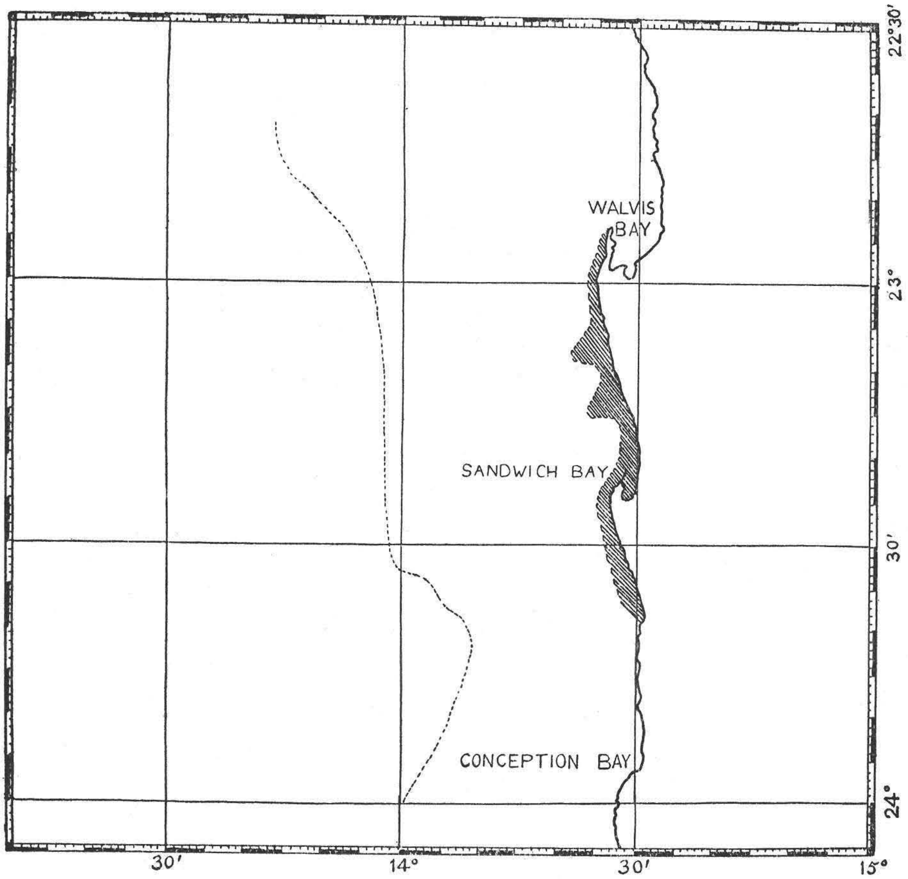

Fig. 1.

Azoic zone near Walvis Bay.
Area between broken lines: approximate extent of azoic zone. Shaded area: sandy strip between the azoic zone and the coast where flora and fauna abound.
(After VON BONDE, 1928b, pl. 4.)

The loss on ignition of the dried sediment amounted to 19.65 % in 2 samples examined by COPENHAGEN. One of these samples was collected in the bay itself, the other being a composite sample prepared by mixing 11 samples, which were all similar in appearance, and which had been collected from various points outside the bay. In the previously mentioned sample of the lower H_2S content (taken close inshore, and containing much sand) the loss on ignition was much lower (3.68 %). As carbonates are completely absent (COPENHAGEN et al., 1934, p. 11) and, therefore, did not contribute to the CO_2 escaping during ignition, the ignition loss will give a fairly exact impression of the organic content.

I must stress the fact that the peculiarities of this sediment are not caused by stagnation of the lower water layers. Besides in the Walvis Bay itself the sediment occurs in the open sea outside it; and there is, as far as I am aware, no barrier whatever. Before explaining what indeed causes the peculiarities of the sediment I shall deal more explicitly with the real cause of the mass mortality.

CHAPTER II.

Particulars concerning the Walvis Bay mortality.

The cases of mass mortality I found in literature are mentioned below; they concern the bay itself, unless mentioned otherwise.

1837, April?: ALEXANDER, 1838, p. 79. Dead fishes observed by ALEXANDER on 19th April; exact date of mortality unknown. According to PECHUEL LOESCHE (in: BREHM, 1920, p. 65) ALEXANDER observed that the whole beach was covered with dead fishes of all sizes. However, all ALEXANDER (l.c.) himself remarks in this respect is the following: "Along the shore of the southern creek were long lines of dead mullet and catfish".

1849?: CHAPMAN, 1868, p. 393; case mentioned only, not observed by CHAPMAN himself. With reference to the mortality of 1860 CHAPMAN remarks: "A similar phenomenon has occurred eleven years ago, when thousands upon thousands of fly-blown fishes lay scattered all over the plain breeding a pestilential atmosphere that was quite unbearable."

1851, December: shortly after the 5th of December, the date ANDERSSON arrived at Walvis Bay a great mortality took place. As a result the water of the bay was covered with a nearly coherent mass of fishes of various species. Live specimens were no more present. ANDERSSON, 1858, p. 268; PECHUEL LOESCHE, 1886, p. 824; STAPPF, 1887 a, p. 55; idem, 1887b, p. 208; BREHM, 1920, p. 65.

1860, December; (approximately at Christmas time): Some days after the 17th of December an enormous mortality took place; thousands of fishes were washed up dead on the shore. CHAPMAN, 1868, p. 393.

1880, 21—23 December: Extraordinarily great mortality lasting for three days observed by Mrs. KOCH at Swakopmund (fide GILCHRIST, 1914, p. 20). At Walvis Bay the mortality commenced one day later: PECHUEL LOESCHE, 1886, p. 824; STAPPF, 1887a, p. 55; idem, 1887b, p. 208; BREHM, 1920, p. 65. Mortality was observed on a minor scale at Sandwich Harbour: KOCH in GILCHRIST, l.c.

1881, Christmas: PECHUEL LOESCHE, 1886, p. 824. After recording the great mortality of December 1880 PECHUEL LOESCHE mentions: "Wiederum zur Weihnachtszeit des nächsten Jahres wiederholte sich der Vorgang in etwas schwächerem Grade." BREHM (1920, p. 65) in citing this passage erroneously omits the words: "des nächsten Jahres", thus giving the impression that the following mortality occurred at Christmas 1880 instead of 1881.

1882, January: ARBUTHUDT, 1882, p. 38 (fide REUNING, 1925, p. 91).

1883, December: STAPPF, 1887a, p. 55; idem, 1887b, p. 208.

1884, December: STAPPF, 1887b, p. 208; SCHULTZE, 1910, p. 164.

1888 or 1889: GÜRICH, 1895, p. 20.

1920, 10 December: mortality observed by Woermannlinie: REUNING, 1925, p. 91.

1924, December: Extraordinarily great mortality according to "Die allgemeine Zeitung, Windhuk" d.d. 22–XII–1924 (fide REUNING, 1925, p. 91). This refers to the same mortality as that mentioned by ANONYMOUS (1926, p. 24); the latter gives two photos of the mortality. WEIGELT (1930, p. 340) gives two photos taken by a teacher KNABBE (Knobbe is a misprint) of a great mortality in 1925. One of these

photos (pl. I, fig. 3) is the same as that given by ANONYMOUS, 1926 on p. 24. Therefore, WEIGELT's record may refer just as well to the mortality of December 1924.
According to CLASSEN (1930, p. 12) the date of the very great mortality is 1923; a photo of the mortality is given. DREVERMANN (1931) gives the same photo (mentioning that he borrowed CLASSEN's block), but with the explanation: mortality of 1926/1927. Probably the dates of CLASSEN and of DREVERMANN both are incorrect. Dr. J. P. S. MCCONNEL, surgeon i.c. hospital at Walvis Bay informs me that the very great mortality occurred with certainty in the southern summer of 1924/1925.

1925, 23—24 December: A quantity of fish washed ashore near the jetty of Walvis Bay and in the lagoon on the following day. Dead fish collected by the South African Fisheries and Marine Biological Survey (VON BONDE, 1928a, p. 42).

1927, January: A small occurrence observed by CLASSEN (1930).

1928, 13 February: A small occurrence observed by MARCHAND (1928, p. 3).

1929: A great mass of dead fish observed by a British steamer 180 seamiles off the coast of Southwest Africa: SCHNAKENBECK (1930, p. 410).

1938, November: A limited mortality occurred shortly before the 24th. Dead fish observed by the authoress on 24th November.

1943, about January: A tremendous mortality which extended right down the coast from Walvis Bay as far as Conception Bay fide Dr. MCCONNEL (in litt.).

One must not conclude from the records given above that in several years no mortality occurs at all. The data are mostly records of travellers who by chance saw or heard of the mortality. According to CLASSEN (1930) some mortality occurs every year; it may even appear 4 or 5 times a season. The very great mortalities occur, however, in some years only.

The mortality takes place in the southern summer. The great mortalities always seem to occur in December (SCHULTZE, 1907, p. 9 fide KAISER, 1930, p. 15; SCHULTZE, 1910, p. 64), and especially about at Christmas time. Extraordinarily great mortalities occurred on 22-XII-1880, in the southern summer of 1924/1925 and in January 1943. The following description of the 1880 mortality (observed by Mrs. KOCH; see GILCHRIST, 1914, p. 20) will give some idea of the extent of such heavy cases: "saw hundreds of living and struggling ("zappelende") fish cast up on the sand by each wave. They were of all sizes and kinds, and included large Dogfish. This continued for three days; the fish lay as far up as the sand dunes, a half to three quarters of an hour's walk behind the houses ..., and were heaped to a height of one or two feet. On Christmas eve it was almost impossible to proceed to the church on account of the odour, and it was scarcily possible to walk about without stepping on the dead fish, which lay behind the houses close up to the doors. The *Lewis Alfred* was in the bay at the time, but the water was so blood-red ("blütig") and smelt so badly that she left for Sandwich Harbour, where fewer fish had been cast up. The stench became so great that it would undoubtedly have caused illness had it not been for the South-west wind, which springs up almost every afternoon. It was useless to think of attempting to bury those millions of fish. Some English and Swedes attempted this in the case of the larger fish, but the fish, specially Harders, continued to be cast up anew. Everything of a white colour became black, even the deck houses of the *Lewis Alfred*, which had returned after three weeks to discharge her cargo. The odour of the dead fish had been felt on board at Usapf. After a few months the skeletons on the shore in the neighbourhood of the lagoon formed a pile five to six feet in height." ... "We fell ill the whole day on account of the smell, and it is surprising that it could have been endured for six months. It was only in September that it became bearable." According to PEÇHUEL LOESCHE (1886, p. 824) on the beach of Walvis Bay the wall of fish was of man's height. Visiting the bay in 1884 he observed that the surroundings of the bay were still paved with fish skeletons.

The extraordinarily great mortalities, as they occur in some years only, are very interesting from a paleontological point of view, because they will leave evident traces in the sediment. During the very great mortality of December 1924 the sardine schools just had entered the bay and, therefore, the millions of dead fish consisted for the greater part of sardines (ANONYMOUS, 1926). Traces of similar events occur in fossil deposits too, as will be set forth in another paper.

Except in the surroundings of Walvis Bay mortality occurs in other places along the coast of Southwest Africa too. L. (1928) mentions that mortality has been observed in several bays along this coast. According to PECHUEL LOESCHE (1886) it never occurs at Sandwich Harbour. From the above mentioned statement of KOCH (in GILCHRIST, 1914, p. 20) that in December 1880 fewer fish had been cast up at Sandwich Harbour, it is apparent, however, that in years of very great mortality it occurs in that harbour too. At Swakopmund mortality occurs also, but in a much lesser degree than at Walvis Bay (MCCONNEL in litt.). If HESSE's statement (1924, p. 185) is right, mortality occurs even as far north as Great Fishbay. Besides in the bays mortality may occur also in the open sea (see for instance the record given by SCHNAKENBECK, 1930). In normal years the mortality seems to be rather local in occurrence. In years of great mortality, however, it occurs along a great part of the coast; in 1943 from Conception Bay right down to Walvis Bay.

The animals drifted ashore consist nearly exclusively of fishes. In some years a great mortality among fish eating birds occurs too. GÜRICH (1895, p. 157) mentions a great mortality among cormorants and penguins in Walvis Bay, December 1889.

It must be ascertained if the mortality occurring repeatedly among fish, birds and seals at the Guano islands laying off the S W African coast (GILCHRIST, 1914, p. 14) has a similar cause as the Walvis Bay mortality. An enormous mortality among seals occurred about 1825 at the coast of S W Africa; great areas being covered with a coffeebrown mass containing a large quantity of phosphoric acid deriving from the thousands of dead seals (SCHULTZE in: MEYER, 1910, p. 166).

The duration of a mortality is 1—3 days. On the first day the fish drifted ashore almost exclusively belong to benthonic living species; on the following days no more benthonic forms come ashore any more, but various pelagic species are cast on the beach (CLASSEN, 1930, p. 11). "It is interesting to note that bottom feeding fish, such as soles, are affected first and later only the surface fish" (MARCHAND, 1928, p. 3).

The fishes collected 24th December 1925 by the Fisheries and Marine Biological Survey are the following [1] (VON BONDE, 1928a, p. 42):

Anguilla spec.	*Pomatomus saltatrix*	*Galeichthys feliceps*
Trigla peronii	*Dentex* spec.	*Rhinobatis*
Epinephelus spec.	*Trachurus trachurus*	*Raia* spec.
Pristipoma operculare	*Mugil* spec.	

The specimens of fish collected by Dr. L. D. BRONGERSMA and myself on 24–XI–1938 on the beach of Walvis Bay for the Rijksmuseum van Natuurlijke Historie at Leiden and identified by Dr. F. P. KOUMANS are the following:

Oxystomus serpens (L.)	*Rhinobatis blochii* M. et H.
Atherina breviceps C.V.	*Dasyatis pastinaca* L.
Mugil saliens Risso	*Mustelus mustelus* (L.)
Galeichthys feliceps C.V.	*Mustelus canis* (Mitchill)

This list does not contain all the species present on the beach, as several of them were in too bad a state to be preserved.

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[1]) To prevent confusion the animals mentioned on this and on the following pages are denominated exactly as in the cited paper (that is: the same name and with or without the author of the genus or species).

CHAPTER III.

The cause of the Walvis Bay mortality.

Various hypotheses have been put forward as to the cause of the mortality; these may be classified as follows:

1. DISEASE.

A peculiar epidemic: CHAPMAN, 1868, p. 393.

Either poisoned or attacked by some disease: ARBUTHUDT, 1882, p. 38.

"Seuchen": STUTZER, 1931, p. 309.

This hypothesis is very unlikely and has no foundations whatever.

2. VOLCANISM.

Popular opinion at Walvis Bay; KOCH in: GILCHRIST, 1914, p. 21; WEIGELT, 1930, p. 309.

The popular opinion among Walvis Bay inhabitants is, that volcanic phenomena, socalled eruptions, are responsible for the mortality. One of the arguments for this conception is the appearance of a mud island in 1900. According to WALDRON (1901) the island appeared in the bay just off Pelican Point (the peninsula that borders the bay) on 1–VI–1900; after some days a great part of the island had already disappeared in the water and on 7–VI it had vanished completely. The surrounding water was dirty, not warm; the odour of H_2S was perceptible as far as Swakopmund. The island must have been a mudvolcanoe, a phenomenon that has nothing to do with volcanism.

The nonvolcanic origin of the island, and also of the fish mortality has been emphasized by various authors (SCHENCK, 1901; CLASSEN, 1930, p. 1; KAISER, 1930, p. 14). CLASSEN lays stress on the fact that volcanic phenomena are not recorded from this coast and secondly on the seasonal character of the mortality.

According to WEIGELT (1930, p. 309) the mortality observed by KNABBE was due to a floodwave originating in a seaquake. In the explanation of pl. II (in fact it is the explanation of pl. I, for the explanations of I and II erroneously are interchanged) WEIGELT mentions, however, that the mortality was due to a floodwave originating in an undersea volcanic eruption. However this may be (seaquake or volcanic eruption), neither volcanic phenomena nor a floodwave were observed: "von einer Erschütterung hat der Beobachter nichts bemerkt, auch andere haben nichts wahrgenommen. Das Ereignis spielte sich nachts ab, die Fische müssen durch eine Flutwelle ans Land getragen worden sein."

3. H_2S.

Hypotheses brought forward in recent publications agree in the supposition that H_2S is the cause of the mortality. The authors are, however, of a different opinion as to the origin of the gas. The following hypotheses are brought to the fore:

A. Gazes escaping from time to time from mudvolcanoes: STROMER VON REICHENBACH, 1912, p. 305; WEIGELT, 1927, p. 39.

B. The H_2S would derive from sulphur compounds of the land, the coast region being very rich in sulphur minerals. The periodicity of the mortality is explained by the periodical rainfall in the hinterland and consequently by the periodical emanating of water from the Kuiseb river on the bottom of the Walvis Bay (Kuiseb underground water hypothesis) (MARCHAND, 1928).

The rivers along this part of the coast are dry erosion beds nearly the whole year round. After times of heavy rainfall in the hinterland the Kuiseb carries water in its upper course; near the coast, however, this river disappears in the sandy soil. Only in exceptional years it reaches the coast overground; normally the communication with the sea is by seepage only (see further p. 27). According to MARCHAND after heavy rains in the hinterland the head of underground water formed by the flooded upper course no longer seeps through the porous layers but bursts through with great force, violently stirring up the bottom deposits and setting free noxious compounds and gazes fatal to fish; in this way causing the death of millions of them. Independently of MARCHAND, CLASSEN (1930) proposed nearly the same hypothesis. CLASSEN's hypothesis was published for the first time by L. (1928, p. 66). REUNING (1925) is also an adherent of the Kuiseb underground water hypothesis. The quantity of sulphur compounds in the river water seems, however, not sufficient to this author; therefore, REUNING supposes that beds of pyrites are present beneath the bay, and that H_2S deriving from these beds comes to the surface with the periodically ascending Kuiseb water.

KAISER (1930) opposing to the Kuiseb underground water hypothesis remarks that the mortality occurs at the time of the first rainfall in the hinterland. By this rainfall the groundwater level in the dry river beds near the coast is not markedly influenced. According to this author the real raining period does not come in December, but some months later, and, therefore, the mortality cannot have anything to do with the rainfall. The hypothesis is also opposed by COPENHAGEN (1934, p. 10), who remarks that it is unlikely that the whole azoic zone, an area of over 5000 square miles should derive its H_2S content from the slight amount of river water reaching the sea in this region.

C. According to KAISER (1930) the H_2S is both the cause of the mortality and the result. Once a mass mortality of fish must have taken place in the bay, the cause of which is not known. H_2S and other decomposition gazes originating from the dead bodies sometimes will ascend in the water and will be the cause of a new mortality. In this way the event will repeat itself again and again.

SCHNAKENBECK (1930) opposes KAISER mentioning inter alia that the mortality is not confined to the bay at all.

D. COPENHAGEN (1934) brought to the fore that the sulphur compounds of the azoic zone are not derived from the land: "Analytical figures of river waters and boreholes from the coast line of South West Africa under consideration show that (1) no sulphides occur, and (2) that in no instance is the sulphate content anywhere approaching half that found in sea water." According to this author the H_2S is formed by reduction of sulphates present in the watery sediment under influence of organisms of the type *Vibrio aestuarii* (cf. BAARS, 1930; KLUYVER, 1931, etc.). Periodically, i.e., in the summer months gas would escape in great quantity and would cause the mass mortality of fish.

That the H_2S of the azoic zone has not been transported there by rivers, viz., that it does not originate from the sulphur compounds of the land, but that it results from reduction of sulphates of the sea water, is certainly correct. However, I cannot agree with the hypothesis, that H_2S is the cause of the fish mortality.

4. Noxiousness of red water of dinoflagellates (probably a poison produced by the living plankton) is in my opinion the real cause of the mortality. The periodicity of the phenomenon then is caused by the fact that great outbreaks of red water occur especially in that time of the year, when the temperature of the surface water is relatively high. The heavy outbreaks of red water in their turn are possible by the presence of upwelling water.

It is a noteworthy fact that shortly before and during the mortality the water has a blood red colour. This peculiarity is cited by most authors, but little attention has been paid to this fact in relation to the explanation of the fish mortality. I found the following data concerning observations of red or yellow-brown water connected with mass mortality in this region:

I. "the water had a reddish colour without any apparent cause" ... "At night time the sea flashed with phosphoric scintillations" (CHAPMAN, 1868, p. 393 speaking about the fish mortality of December 1860 at Walvis Bay).

II. "the water was so blood-red" observation of Mrs. KOCH during the great mortality in December 1880 at Swakopmund (GILCHRIST, 1914, p. 20).

III. "Am 21. Dezember 1880 gewährte man auffällige dunkelrosa Streifen im Wasser der Bai. Nächsten Tages begann ein erschreckendes Sterben" ... "Wiederum zur Weihnachtszeit des nächsten Jahres wiederholte sich der Vorgang in etwas schwächerem Grade. Um Weihnachten 1883 wurden nochmals die rothen Streifen im Wasser bemerkt, es trat jedoch kein Fischsterben ein" observed at Walvis Bay (PECHUEL LOESCHE, 1886, p. 824).

IV. "Another remarkable fact is this that during such occurrences of fish mortality the water along this area of the coast is of a blood red colour." (MARCHAND, 1928, p. 3).

The occurrence observed by MARCHAND February 13th 1928 is described in the following way: "On this particular morning, before daybreak, my attention was drawn to the fact that shoals of mullet and massbankers were swimming about lethargically on the surface, and taking no notice of innumerable sea-birds which were catching them by the dozen. The water of the bay was streaked with lanes of a blood red colour (subsequently proved to be due to masses of *Noctiluca*). The fish which consisted chiefly of Golden or Flathead Mullet (*Mugil auratus*) and Massbankers (*Trachurus trachurus*), were swimming lazily on the surface in shoals, rapidly opening and shutting their mouths as if finding difficulty in breathing. They could be picked out of the water by hand with the greatest ease."

V. "Das Wasser der Walfischbucht hatte an dem Morgen eine eigenartige gelbbraune Färbung, so wie sie Herr Knobbe bereits einige Monate vorher einmal an der Swakopmunder Mole beobachtet hatte" observed by teacher S. KNABBE at the 1924/1925 mortality (WEIGELT, 1930, p. 309 under death by volcanism).

VI. "Bei ruhiger See und leichtem Seewind sah man plötzlich auf dem grünblauen durchsichtigen Wasser der Bucht braune oder blutrote Wolken auftreten, die sich scharf von der vorherrschenden Farbe des Wassers abhoben" observed by CLASSEN (1930) at the commencement of a fish mortality in 1927.

Probably the following observation by GÜRICH (1895, p. 159) points to the same phenomenon, though the explanation of the cause of the red colour in all probability is incorrect: "von den massenhaften Exemplaren und Fragmenten an letzteren [= jellyfishes] erschien das Wasser der Bai und der See meilenweit blutroth gefärbt." The same applies to the remark WEIGELT's (1927, p. 203) that the mortality is caused by "einer roten Milbe". PECHUEL LOESCHE (1886, p. 824) although stating that volcanism is the cause of the mortality, mentions in a footnote that according to C. WILMER, an inhabitant of Walvis Bay, a red alga causes the mortality. With the exception of STROMER VON REICHENBACH (1896, p. 121) later authors neglected this remark.

GILCHRIST (1914, p. 19) mentions the Walvis Bay mortality under the heading death by submarine disturbances, giving the explanation of Mr. KOCH. GILCHRIST himself inclines, however, more to another view, that is pollution of the water by diatomaceous matter. Although stating that red water of dinoflagellates in other places (e.g., along the Cape Peninsula) may cause mass mortality and moreover that the water at the December 1880 mortality at Swakopmund was red indeed, GILCHRIST arrives at the conclusion that not red water of dinoflagellates, but decay of diatomaceous matter in the bottom of the bay is the main factor causing the occurrences in the Walvis Bay region. To support this hypothesis he states "that the colour of the water was described by another observer some months after the December 1880 mortality as "inky" ... This, together with the fact that at the somewhat similar occurrence in the neighbourhood (Walfisch

Bay) there is no mention of red water, seems to indicate that, if present, it was not the main factor in the disturbance at Swakopmund." (GILCHRIST, 1914, p. 31). It will be obvious, that it is of no great value what was the colour of the water (and with that probably the nature of the plankton) some months after the mortality; and further there is a record of red water during the December 1880 mortality at Walvis Bay too (see above, observation III).

MARCHAND (1928) after defending the Kuiseb underground water hypothesis adds at the end of his paper, that during occurrences of fish mortality the colour of the water is bloodred and continues: "Now some writers have suggested that this is also due to the flood waters from the rivers. Such, however, is not the case, for I have seen this red water and have taken some of it and examined it under the microscope when the red colour is revealed to be due to masses of a species of phosphorescent organism, viz., *Noctiluca*. Such red water occurrences are quite common on the South African Coast. "Dark water", due to masses of diatoms in the sea is also seen quite often on this part of the West Coast and I would suggest here, that sometimes minor occurrences of fish mortality are due not to the setting free of noxious compounds and gases from the bottom, but to vegetable decay of these masses of *Noctiluca* and diatoms polluting the water."

I do not agree with MARCHAND in the following respects: In the first place not minor, but all periodically occurring mass mortalities in this region are caused by mass development of plankton organisms. Secondly in MARCHAND's opinion the noxious effect is pollution of the water by a great mass of dead plankton; it being indifferent whether dinoflagellates are present or a mass of other dead plankton organisms, e.g., diatoms. The mortality occurs, however, only during occurrences of red water; and, therefore, only red water organisms (very probably when they are still alive) are responsible.

Only by an exact study of the plankton all the year round my hypothesis may be proved. This being impossible during the war I searched for another proof, which I found by raising the following question: If in the Walvis Bay area upwelling water creates the circumstances for great outbreaks of red water, and in its turn red water causes mass mortality of fish, does one find in other regions of upwelling water fish mortality caused by red water too? To answer this question I made a study of all the literature concerning cases of fish mortality and of red water. The answer, that will be discussed below, proves to be in the affirmative.

CHAPTER IV.

Upwelling water and other cases of ascending motion.

The purpose of this paper is to emphasize the importance of regions of upwelling water with regard to oil geology and to vertebrate paleontology. Therefore, it is worth while to give a short survey of the localities, where upwelling occurs, and of their peculiarities. Upwelling implies that subsurface water is continually or intermittently drawn to the surface, and is spreading outward from the area of upwelling (SVERDRUP & FLEMING, 1941, p. 318).

Upwelling occurs in regions of diverging currents; that are regions where surface water masses flow away from each other or away from a coast. These divergences may be present anywhere in the sea; they are, however, particularly conspicuous along certain coasts (SVERDRUP, 1938; SVERDRUP, JOHNSON, FLEMING, 1946, p. 140, 787).

I. DIVERGENCES NEAR COASTS.

Upwelling occurs at some coasts, where the surface water under influence of the prevailing wind is directed off from the coast. The direction of the prevailing wind itself need not to be offshore; for under influence of the earth's rotation a wind current turns off to the right of the prevailing wind on the northern hemisphere and to the left on the southern hemisphere, and therefore, even if the wind is not directed offshore, the surface water may still get a markedly offshore direction. The deficit of surface water originating in this way near the coast is replenished by subsurface water.

Formerly it was surmised that upwelling water came from a very great depth. Recent investigations have shown, however, that upwelling water derives usually from depths not exceeding 200—300 m (SVERDRUP, 1930, 1938; SVERDRUP & FLEMING, 1941; DEFANT, 1936; GUNTHER, 1936*a*). Deep water does not rise to the surface, but an overturning of the upper layers takes place (SVERDRUP, JOHNSON, FLEMING, 1946, p. 501).

Upwelling is an unstable phenomenon; it does not occur incessantly, being dependent upon the strength, the direction and the constancy of the wind. The most important regions of upwelling occur where the direction of the wind is fairly constant during the whole or during a part of the year (trade winds, monsoon winds). The most important regions of upwelling are, therefore, to be found in the subtropics and in the tropics.

Upwelling occurs on the following coasts (figs. 2 and 3):

Atlantic Ocean: S W Africa (DEFANT, 1936); Gulf of Guinea, chiefly between 5° W and 5° E (Gold- and Togo coasts) (JANKE, 1920; BÖHNECKE, 1943); N W Africa (BÖHNECKE, 1936, 1943; DEFANT, 1937*a*, 1937*b*, 1939); a narrow strip along the Iberian Peninsula (BÖHNECKE, 1943); part of the coasts of Venezuela and Colombia (SCHOTT, 1902, 1931*a*, 1932*a*); coast of Brazil near Rio de Janeiro and a limited region near Bahia (BÖHNECKE, 1943).

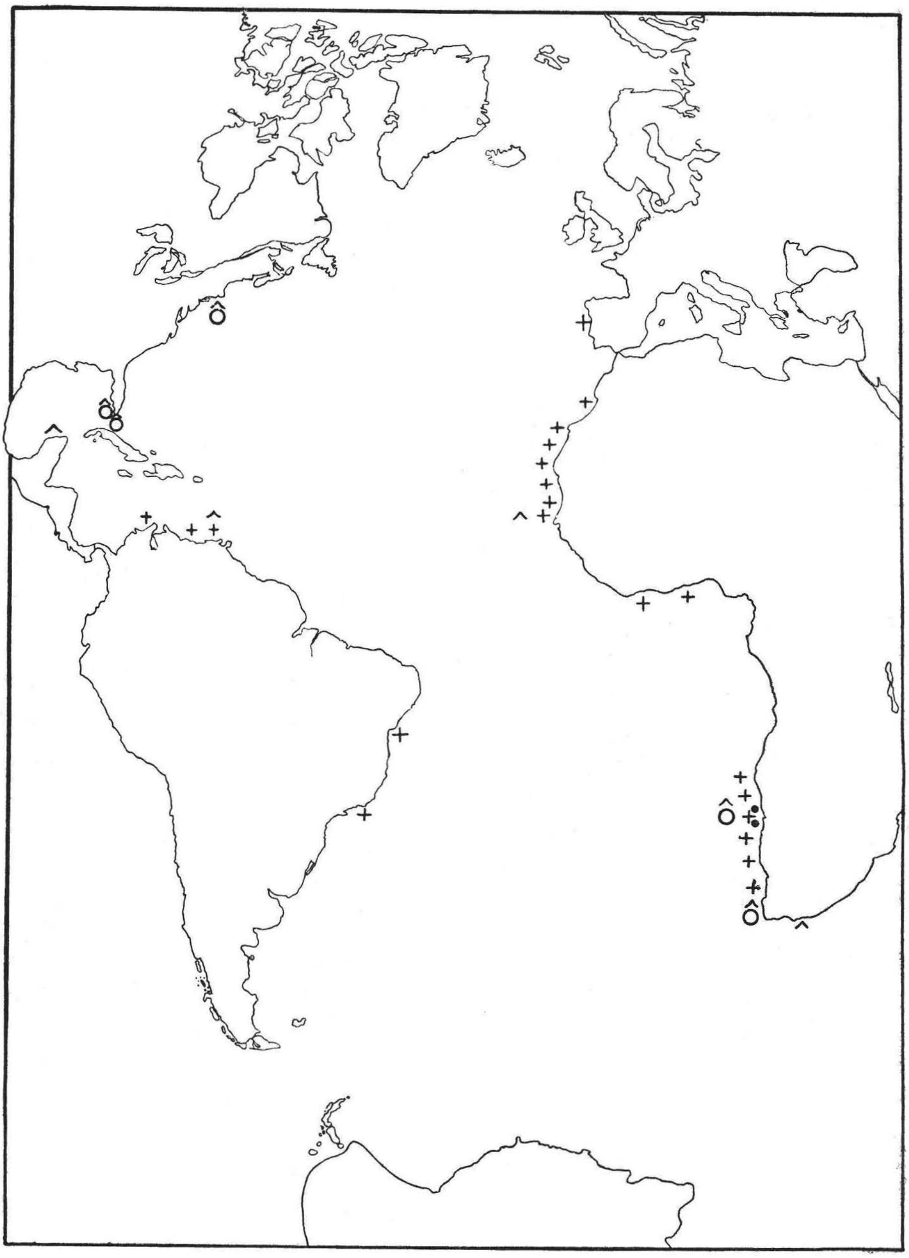

Fig. 2.

Occurrence of upwelling water, red water, mass mortality and diatom ooze in the Atlantic Ocean.

+ upwelling water; o red water; ⋀ mass mortality; ô red water accompanied by mass mortality; ● diatom ooze, broad band of diatom ooze in the antarctic region not indicated.

Fig. 3.

Occurrence of upwelling water, red water, mass mortality and diatom ooze in the Indian and Pacific Ocean.
+ upwelling water in northern summer; — upwelling water (only) in northern winter; o red water; Λ mass mortality; ô red water accompanied by mass mortality; ● diatom ooze, broad bands of diatom ooze in arctic and antarctic regions not indicated.

Indian Ocean: coast of Somaliland south of Cape Gardafui; surroundings of Aden and Perim and further eastwards along the Arabian coast to Cape El Hadd; southern coast of Ceylon (SCHOTT, 1935).

Pacific Ocean: Peru and the northern part of Chile (SCHOTT, 1931*b*; GUNTHER, 1936*a*, 1936*b*; SCHWEIGGER 1943, 1945*a*, 1945*b*); California (MCEWEN, 1912, 1934; MICHAEL, 1921; MOBERG, 1928; SVERDRUP & FLEMING, 1941; SVERDRUP, JOHNSON, FLEMING, 1946); Gulf of Panama (SCHOTT, 1931*b*, 1935).

The phenomenon of upwelling is surely not equally important in all regions mentioned above. In some of them the degree of upwelling, the time during which upwelling takes place and the extent of the region are rather limited. The four regions of upwelling at the west coasts of the continents (S W Africa, N W Africa, Peru-Chile, California) are certainly the most important on earth, especially those in the southern hemisphere. They are situated in the subtropics; the Peruvian area reaches into the tropics.

Upwelling may also occur at the coasts of great inland seas (E coast of the Caspian near Kuuli ?, FICKER, 1920), or of semiseparated parts of the ocean, for instance parts of the coasts of the Red Sea (THOMPSON, 1939).

II. DIVERGENCES IN THE OPEN SEA.

Atlantic Ocean: Divergences occur in the S W and N W directed offshoots of the Canarian Current and the Benguella Current respectively. According to BÖHNECKE (1943) the low temperature of these regions cannot be merely the result of cold water horizontally adduced from the regions of upwelling near the coast, but for the greater part must be due to ascending motion in mid ocean along the line of divergence. Another divergence occurs in mid Atlantic somewhat north of the Azores.

Pacific Ocean: At the northern border of the Equatorial Counter Current a divergence occurs at 10° N and a second one at the equator (SVERDRUP, JOHNSON, FLEMING, 1946, p. 711).

Notwithstanding that the depth from which water is drawn to the surface is not very great, upwelling water differs in many respects (temperature, salinity, concentration of nutrients) from normal surface water. The temperature is comparatively low and the concentration of nutrients is very high (the latter will be described more in detail in chapter VIII). Moreover, cold upwelling water has a marked influence upon the climate of the hinterland.

Besides upwelling there are other ascending currents too. As their effect with regard to the supply with nutrients is somewhat analogous, they will be mentioned briefly: The most important region of ascending currents is the Antarctic Ocean. In this region the ascending water does not derive from a very limited depth, but deep water ascends. Southward flowing deep water gradually climbs from a depth of 3000 m to within 200 m of the surface. It does not appear to reach the very surface (SVERDRUP, JOHNSON, FLEMING, 1946, p. 618), but within the entire Antarctic region a considerable amount of the ascending water is added to the surface layer (SVERDRUP, 1933; DEACON, 1937). This water flows gradually northwards to sink to deeper layers at the Antarctic Convergence; the mean latitude of the Convergence being 53° S (for exact positions see MACKINTOSH, 1946).

Ascending motion may also occur where submarine ridges cause bottom currents to be deflected upwards, e.g., at the ridge between Cape Gardafui and the island of Socotra (GILSON, 1937), etc.

Finally the following must be mentioned: In density currents heavy (and with that usually cold) water occurs to the left of an observer looking in the direction of flow on the Northern hemisphere; on the Southern hemisphere it lies on the right hand side. In strong density currents the isopyknes (and with that usually the isothermes) show a very oblique direction, rising from a depth of some hundred metres to or near to the surface (see figs. 6*a* and 6*b*).

According to DIETRICH (1935*a*, p. 57) this ascending of cold water ought to be termed "dynamically caused upwelling" in contradistinction to the upwelling caused directly by winds. To use the word upwelling in this connection is somewhat confusing, because there is no continuous ascending motion. Sometimes the isopyknes slope somewhat more than at others, and therefore, there may be some ascending or descending motion, but this has nothing to do with upwelling. Still the occurrence of water from deeper layers on a high level will have an important biological effect (somewhat analogous to that of upwelling), at least in those cases that the deeper water layers with a high nutrient content are raised to or very near to the well lighted surface. This occurs occasionally in very strong density currents. The Gulf Stream System is the strongest density current on the Northern hemisphere, the Agulhas Current (probably) on the Southern hemisphere (DIETRICH, 1936, p. 230). Therefore, "dynamically caused upwelling" occurs sometimes at the coast of S Florida (DIETRICH, 1936, 1937) and along the coast of the Union of S Africa (DIETRICH, 1935*a*, 1935*b*, 1936).

Of the most important regions of upwelling and of the situation in the Agulhas and Florida Currents a short description is given here.

In order to compare the degree of upwelling in various localities different methods of estimating have been adopted. The method most used consists in noting the deviation of surface temperatures near the coast from the thermal normal for the latitude (temperature anomaly); the disadvantage of this method being that the temperature of the water is not influenced by upwelling alone, but that it is intimately connected with the character of the current. This difficulty is partly overcome when comparing the temperature near the coast with the mean surface temperature at a distance off the coast, just beyond the influence of upwelling. These values are given by BÖHNECKE (1943) for regions of upwelling in the Atlantic. Besides these values I shall also give those calculated by the first method, to facilitate a comparison with regions of upwelling in other oceans.

ATLANTIC OCEAN.

1. S W AFRICA.

North of about 25°—30° S the trade wind blows nearly the whole year round from a southeasterly, near the coast more southerly direction. A divergence has developed nearly along the border of the shelf chiefly from about 30° to 20° S. Between this divergence and the coast an overturning of the upper water layers (= upwelling) takes place. Besides this transverse circulation the rather weak current has a northerly direction (DEFANT, 1936) (see fig. 4). Upwelling occurs nearly as far north as Great Fish Bay (SCHOTT, 1942, p. 242).

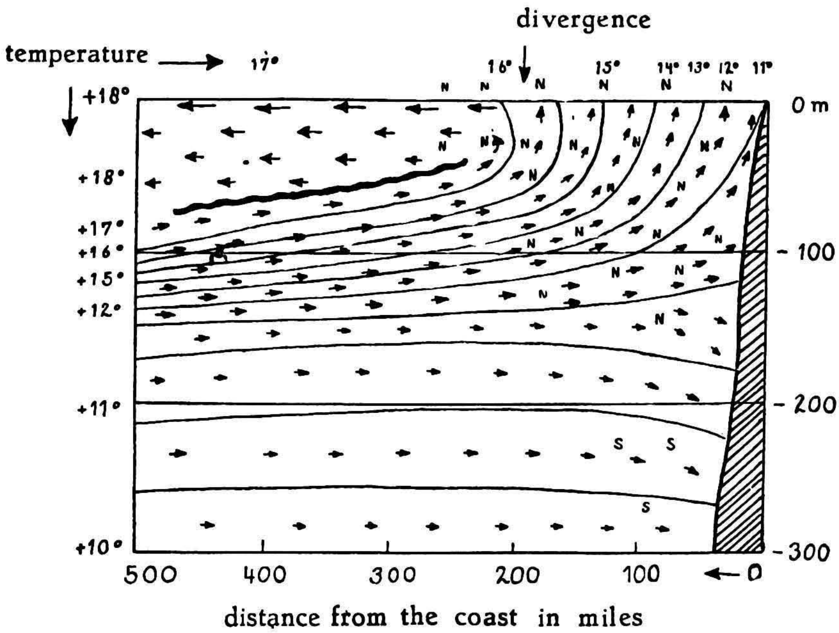

Fig. 4.

Schematic section at right angles to the coast of SW Africa. Drawn lines: isopyknes (lines of equal density). Arrows: Vertical and zonal (= at right angles to the coast) components of motion. Letters: Components of motion parallel with the coast (*N* northern component; *S* southern component). Undulated line: Axis of vertical water movement. (Vertical exaggeration 1 : 2300.) (After DEFANT, 1936, fig. 7.)

The negative temperature anomaly of the coastal water occurs all the year round. The maximum anomaly is during the whole year of nearly the same range (—8° to —10° C). The region of maximum anomaly shifts, however, during the course of the year in a north south direction. In summer (January) it is present much more southerly than in winter; in summer it lies between 30° and 23° S and in winter between 27° and 16° S (figs. 5*a* and 5*b*).

At the latitude of Swakopmund (situated a little north of Walvis Bay, at 23° S) maximum upwelling occurs in May, and minimum upwelling in midsummer (December/January). The increase in temperature from the coast westwards until 5° E (where upwelling is no more discernible) amounts to 7° C in May and to 3.5° C in December/January (BÖHNECKE, 1943). Therefore, although in the southern summer upwelling is still rather important as far north as the azoic region, the degree of upwelling is much less and, as a result the water becomes much warmer at the end of the year.

The cold upwelling water quite close to the coast has a marked influence upon the climate of the hinterland; it causes nearly complete rainlessness

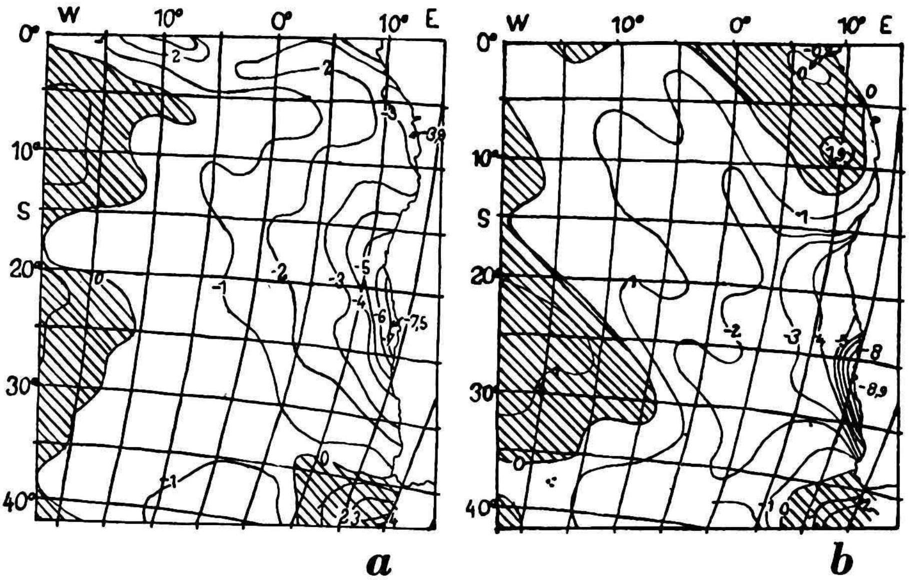

Fig. 5.

Temperature anomaly of the surface water near the coast of SW Africa. *a*. July; *b*. January. After Defant, 1936, fig. 1.

of the coast region. The air often has a fairly high degree of humidity, but condensation to rain does not take place. Mist is a frequently occurring phenomenon. Dense mist banks lie nearly permanently over the cold coastal water. At night, especially in the southern winter, when the desert cools down considerably, the mist banks penetrate far over the land. In the course of the night the landwind rises pushing the humid air back to the sea. Therefore, the humidity of the air may be very high; the soil, however, remains dry. These peculiar deserts in the hinterland of regions of upwelling water are called by KÖPPEN (1932; 1934*a*) humid air deserts.

In some regions of upwelling the high humidity of the air leads to the development of a peculiar vegetation: the Lomas of Peru are bound to the mist area along the coast; the same applies to the very hygrophile *Sequoia sempervirens* forests of California. In the extremely arid climate of SW

Africa, however, the high humidity of the air is of very little value to the vegetation, because the soil is too dry (WALTER, 1937). As a result the vegetation is nearly totally wanting with exception of the river valleys. Notwithstanding the rivers themselves are dry nearly the whole year round, the vegetation in their erosion beds may be rather luxuriant.

The rainlessness applies only to a narrow strip of land along the coast, the socalled Namib. With Namib the Hottentot meant the desert region stretching westward of his meadows to the sea. This definition is taken over in geography and the name Namib is applied nowadays to the whole coast region with desert character from the mouth of the Kunene in the north to the mouth of the Orange river in the south. The average width of the Namib is nearly 60—100 km. Towards the east where the rainfall is considerably higher, it merges almost imperceptibly into the shrub steppe and gras steppe of the interior. The mean annual rainfall in the northern Namib is given by WALTER (1937, fig. 8). At Swakopmund it amounts to 17 mm, at Walvis Bay to 15 mm and at Conception Bay it is only 5 mm. In several years rain fails to come at all; therefore, the Namib belongs to the extremely arid deserts. There are, however, exceptional years in which a considerable quantity of rain falls in the coast region. Such exceptional years were 1892/1893 (DOVE, 1894, 1898) and 1933/1934 (WALTER, 1937). This reminds of similar events on the coast of Peru. As will be shown below rain falls in Peru also only in exceptional years, and this coincides with the ceasing of upwelling along the coast, the northward flowing Peru Coastal Current being replaced by the southward directed Equatorial Current. The events observed in 1934 at the coast of S W Africa have a great resemblance with these phenomena: According to Dr. BOSS, an inhabitant of Swakopmund (in: WALTER, 1937, p. 69) in the southern summer of 1933/1934 the direction of the Benguella Current was reversed; instead of northward it flowed southward. The southern direction was discernible as far south as the mouth of the Orange river. From March until September 1934 the mean temperature of the sea water near Swakopmund was 3° C above normal. In that exceptional year a considerable amount of rain fell in the coast region. The annual rainfall for 1934 amounted to 148.7 mm (121.9 mm in March and 26.8 mm in April) at Swakopmund and to 96.5 mm at Walvis Bay (WALTER, 1937, p. 70). In such exceptional years plants germinate at various parts of the Namib and a rather rich vegetation of succulents, grass, etc., may be met with (DOVE, 1894, p. 43; WALTER, 1937).

The rainlessness and with that the scantiness of the vegetation have a marked influence upon the soil, a great part of the Namib being covered with loose sand that is piled up to high shifting dunes. This sand desert has its greatest width between Lüderitz Bay and the river Kuiseb (see map in WAGNER, 1916); much reduced in width it crosses the Kuiseb between the coast and Ururas and extends as far north as the Swakop, by which the dunes are sharply cut off. North of the Swakop sand dunes occur just as well, but the great shifting dunes fail here nearly altogether. Under influence of the southern trade wind this sand is carried to the north (KAISER, 1926). On stormy days these dunes travel forward at a considerable speed. When the east winds sometimes penetrate the western Namib, great masses of this sand are blown towards the sea. The sand falls, however, on or very near to the coast, because the east wind does not go out over the sea (SCHOTT, 1942, p. 246).

Of the rivers only the Orange river and the Kunene carry water all the year round. The other rivers carry water only during a very short time after heavy rains in the hinterland; usually they are dry erosion beds only. The Namib is traversed by a large number of such intermittent rivers, which take their origin in the interior upland. The mouth and the lower course of these rivers are mostly choked up with sand. Only the large Swakop has been able to keep its channel open down to the sea. The latter "comes down" once in two or three years carrying away all the sand, which in the meantime has been blown into the river bed. Therefore, the shifting dunes cannot pass this river to the north. In years of abnormally great rainfall enormous masses of sand and a great part of the vegetation growing in the river bed is transported to the sea; in 1934 a great number of tree trunks moved downstream (GOETZ, 1936). The Kuiseb comes down on rare occasions only. For the 19th century observations are known from the following years: 1837, 1848, 1852, 1864, 1880, 1885, 1893 (PECHUEL LOESCHE, 1886, p. 825; WALTER, 1937, p. 88). Normally the mouth and the lower course of the Kuiseb have been blocked up totally by sand. The water continues, however, to percolate underground, until it eventually reaches the coast, spreading out in an estuary that reaches according to WAGNER (1916, p. 22) from Sandwich Harbour to Walvis Bay.

As a further result of the rainlessness of the coast region saltpans occur frequently. These are most numerous along the actual sea shore, whereas several smaller pans occur more inland too. The first mentioned represent former bays (GEVERS & VAN DER WESTHUYZEN, 1932, p. 66). Finally the rainlessness combined with the abundance of life in the sea and with that of birds (see chapter VIII) leads to the deposition of guano.

Summarizing one may conclude, that the presence of upwelling water along the coast brings about an extreme desert character of the coast region: rainlessness, scantiness or complete absence of vegetation (except in the river valleys); bottom consisting of loose sand piled up to high shifting dunes; intermittent rivers; saltpans; guano.

2. N W AFRICA.

Upwelling occurs along the Saharian coast, especially between the latitudes of the Canarian islands and the Cape Verde islands. The temperature anomaly may attain a maximum value of nearly — 7° C near Cape Blanco (DEFANT, 1937*a*, p. 250). The mean annual increase in temperature from the coast at Cape Blanco (21° N) westwards until 25° W amounts to 3.2° C. The greatest increase, and with that maximum upwelling occurs in November (4.7° C), in January (3.9° C) and from May to June (3.2°—4.0° C). The minimum increase occurs in August with 1.3° C (BÖHNECKE, 1943).

The region between the Canarian islands and the Cape Verde islands is practically rainless (SCHOTT, 1942, pl. XIV). In this region great masses of fine Saharian sand are blown into the sea. Contrary to S W Africa, where the sand falls in the water quite near the coast, in the Saharian region it is transported far out over the sea; that is even west of the Cape Verde islands (SCHOTT, 1942, fig. 79).

3. COAST OF VENEZUELA AND COLOMBIA (between about 60° and 75° W).

The occurrence of upwelling water at this coast was for the first time shown by SCHOTT (1931*b*; 1932*a*). The mean annual increase in temperature from the coast at 63° W northward to 12°—13° N is 1.8° C. The highest increase and, therefore, the strongest upwelling occurs in summer time (May—September); the maximum occurs in August with 4.1° C, the minimum in March with 0° C (BÖHNECKE, 1943).

As a result of the presence of cold upwelling water the coast region (a narrow belt along the coast between Cumana and Santa Marta) and the islands before the coast have a steppe or even a desert climate (SCHOTT, 1931*a*).

INDIAN OCEAN.

4. RED SEA.

According to THOMPSON (1939) from May to September the winds blow from a NNW direction from the Sinai Peninsula to Bab el Mandeb. From October to April the direction remains unchanged for the northern part of the sea to about 22° or 21° N. South of this latitude the mean direction is SSE in this time of the year.

As a result of the NNW wind upwelling occurs along the whole Arabian side of the Red Sea in summer; along the northernmost part of the Arabian side it occurs even during nearly the whole year. Moreover, in summer an upward movement of subsurface water occurs in the northern part of the open sea.

In the other half year upwelling occurs along the Egyptian coast, but only in its southernmost part. Moreover, in winter an upward movement of water occurs in the southern part of the open sea, just north of the shallow sill near the Hanish islands. This upward moving Red Sea water is probably split by the inflowing Gulf of Aden surface current, one part appearing at the barrier, the other part being carried upwards and backwards and reaching the very surface at about 15° 50′ N (THOMPSON, 1939, p. 97).

5. COAST of SOMALILAND south of Cape Gardafui, and

6. COAST OF S AND SE ARABIA (between Aden and Perim (STEIN, 1933), and also further eastward to Cape El Hadd). This Cape plays according to SCHOTT (1935, p. 218) a similar part as a weather boundary as Cape Gardafui.

At the coasts of 5 and 6 upwelling occurs during the SW monsoon only (May—October). In winter the direction of the prevailing winds is reversed and upwelling does no more occur. The temperature anomaly may attain a value of — 5° C at the coast of Somaliland and of — 4° C at the coast of S Arabia (SCHOTT, 1935) (mean value for August).

7. SOUTHERN COAST OF CEYLON.

According to SCHOTT (1935, p. 224) upwelling occurs during the SW monsoon and ceases with the onset of the NE monsoon.

PACIFIC OCEAN.

8. COAST OF PERU—CHILE.

Upwelling occurs in the Peru Coastal Current. This name was introduced by GUNTHER (1936*a*, p. 109) to denote that part of the South Pacific anticyclonic circulation, in which northerly current is most conspicuous. The extreme southern limit of the Peru Coastal Current must be placed at 40°—41° S. South of this latitude the prevailing wind is WNW in all seasons; therefore, a northerly directed current (and with that the possibility of upwelling) seems not to occur more southerly. The region between 40°—41° S and about 34° S is influenced by the monsoon, and, therefore, the prevailing wind alternates with the season. From October to March it comes from the south and from April to September from the north. As a result in the southern summer the direction of the current is northerly, attended by upwelling; whereas in the southern winter the surface drift becomes southerly, and upwelling comes to a stop. The southern limit of the Peru Coastal Current, therefore, varies with the season (GUNTHER 1936*a*, p. 227).

North of Caldera the direction of the current is influenced by the trade wind. This trade wind blows nearly the whole year round from a southerly direction off Chile, and from a southeasterly direction off Peru. Therefore, the sudden bend of the coast near Arica has according to GUNTHER not such great influence upon the upwelling as would be expected, for off both coasts, Chile as well as Peru, the winds are nearly parallel with the shore. As the wind and the current are stronger and more regular at the coast of Peru than at the coast of Chile upwelling is somewhat more vigorous off Peru, than it is off Chile. According to GUNTHER (1936*a*) there are certain places, where upwelling is more conspicuous than at others. Such centres of upwelling are located at 5° S and 15° S. The temperature anomaly may attain a value of —8° C (SCHOTT, 1935, pl. XXVI) (mean for August).

Like the southern boundary the northern boundary is liable to vary. In the southern winter it lies nearly between Payta and Lobitos. After the summer solstice the situation of the winds and of the currents becomes very labile between 8° N and 5° S. In that time northerly winds enter the southern hemisphere in some years. As a consequence instead of the cool Peru Coastal Current diverging from the shore, hot water of the Equatorial Countercurrent flows southwards and converges with the shore. This phenomenon occurs mostly from Christmas and, therefore, the Countercurrent is called by SCHOTT (1931*b*; 1935) and GUNTHER (1936*a*; 1936*b*) El Niño (= the Christ Child). SCHWEIGGER (1943; 1945*a*; 1945*b*), has emphasized, however, (after having taken into account a great number of observations) that these authors have mixed up two different phenomena:

1. a warm countercurrent coming out of the Gulf of Guayaquil. This current has nothing to do with the occurrence of northern winds. It may be observed only quite near to the coast to about 5° S. It occurs every year in the southern summer and is called since long time by the inhabitants of Payta: El Niño. This current has nothing to do with the catastrophic events (torrential rains, etc.) occurring in some rather exceptional years in northern Peru.

2. an abnormal southward flow of the Equatorial Countercurrent which occurs under influence of northern winds, entering the coast water of northern Peru in some exceptional years only. The latter, that may have catastrophic consequences, is known in oceanographic literature under the name of El Niño (MURPHY, 1926; SCHOTT, 1931*b*; 1935; GUNTHER, 1936*a*; 1936*b*; MEARS, 1944; SVERDRUP, JOHNSON, FLEMING, 1946, etc.). According to SCHWEIGGER (l.c.) the name El Niño should not be given to this current. We shall refer to it as the "false-Niño current".

It is traditionally believed that the false-Niño current occurs nearly once in 7 years. In very abnormal years (possibly once in 34 years; MURPHY, 1926) it may be observed as far south as Pisco (14° S); this obtained in the spring of 1891 and of 1925 (MURPHY, 1926; SCHOTT, 1931*b*, ZORREL, 1928).

The occurrence of warm water in the region of the Peru Coastal Current must, however, not always be interpreted as false or true Niño phenomena. It may also be the result of warm wedges converging with the coast; these warm wedges approach the coast from the open ocean, and, therefore, more from an offshore direction (GUNTHER, 1936*a*; SCHWEIGGER, 1945). This occurs at various parts of the coast of Peru under quite normal circumstances, and, therefore, not in exceptional years only. The warm wedges penetrate to the very coast especially in that time of the year when the Peru Coastal Current is rather weak.

Just as at the coast of SW Africa the cold upwelling water causes an extreme desert character of the coast region. As the upwelling water of Peru reaches into the tropics, a very sharp change in the climate of the coast region occurs at the northern boundary of the Peru Coastal Current: tropical wet climate of Ecuador against the practically rainless climate of Peru. This rainlessness applies to the coast region only; according to MURPHY (1926, p. 27) the seaward slopes of the mountains, as well as the littoral region of the ocean for more than a hundred miles offshore are rainless. In this region it comes to the production of mist or mistrain (garuas) only. Most of the rivers are perennial, but they contain very little water in the southern winter; some rivers are dry during the greater part of the year (Rio de Piura in the Sechura desert, etc.).

As a result of the rainlessness of the coast region the vegetation is very scarce, although the garuas give rise to the development of a peculiar vegetation, Lomas, consisting chiefly of perennial plants (WEBERBAUER, 1911; BRUNS, 1931). This vegetation occurs along the coast especially between 12° and 17° S. It appears at the end of the southern winter, to disappear in early summer. In the northern part of the coast region, where the Lomas are absent, the desert character is still more pronounced.

Coinciding with the phenomenon of the false-Niño current, when upwelling comes to a stop and the cold belt of water is present no longer along the coast, a considerable rainfall may be observed in the coast region of northern Peru. Such years were 1891, 1925 (MURPHY, 1925; 1926), 1932 (KÖPPEN, 1934*b*), 1939 and 1941 (MEARS, 1944). In the very abnormal years 1891 and 1925 rain fell along a great part of the Peru coastal region.

9. GULF OF PANAMA.

In this region upwelling occurs during a quarter of a year only (January to April). SCHOTT supposes that the updraught will be particularly vigorous during heavy northers. Because upwelling occurs during a short period only, the influence upon the climate of the coast region is not very pronounced (SCHOTT, 1931*b*, p. 166).

10. COAST OF CALIFORNIA.

Upwelling occurs in the California Current, that is chiefly between 48°—23° N. NNW winds prevail in this region from March until July; the direction of the prevailing winds changes in midsummer. Due to the NNW winds upwelling occurs in spring and in summer; at the end of the summer it ceases gradually. The most conspicuous centres of upwelling are located in 41° N and 35° N. Probably a third centre of upwelling occurs in about 24° N at the coast of Lower California (SVERDRUP, JOHNSON, FLEMING, 1946, p. 725).

The temperature anomaly may attain a value of — 6° C (SCHOTT, 1935, pl. XXVI) (mean for August).

In W California the precipitation is chiefly confined to the winter months; in summer it is very scanty. Mist is a very frequently occurring phenomenon; it occurs particularly in summer (JONES & BRYAN, 1930). The predominant vegetation is Chaparral (a shrubbery of broad-leaved sclerophylls). Hygrophytic forests, composed chiefly of redwoods (*Sequoia sempervirens*) occur, however, in the mist area along the coast. South of Carmel the forests are confined to valleys (SHREVE, 1927; WALTER, 1937, p. 125).

11. SOUTHERN COAST OF AFRICA (figs. 6*a* and 6*b*).

According to MÜHRY (1862; 1864) only the southeastern side of the Agulhas Bank is dominated by the warm Agulhas Current, whereas the southwestern side is dominated by the cold Benguella Current. This hypothesis was accepted in literature during many years. According to DIETRICH (1935*a*; 1935*b*) the region from Durban on the SE coast to St. Helena Bay on the SW coast is, however, wholly dominated by the Agulhas Current. The latter is chiefly a density current; only in the upper water layers the peculiarities of the density current are partly masked by the wind current. In a depth of 50 m, however, the peculiarities of the density current are already discernible in an unconfused manner. The Agulhas Current flows with great velocity from the Indian to the Atlantic Ocean. On this way the mightiness of the current diminishes rapidly; the greater part of the water returns in anticyclonic whirls to the Indian Ocean, only a small part appears to continue in the Atlantic. The water of the Agulhas Current may be perceived clearly as far north as St. Helena Bay.

As is to be expected in the Southern Hemisphere water of high density occurs on the righthand side of an observer looking in the direction of flow (SVERDRUP, JOHNSON, FLEMING, 1946, p. 696), and, therefore, a narrow belt of cold, heavy water occurs along the continent. In the figure 25 by DIETRICH (1935*a*) representing the isothermes in a depth of 50 m it is clearly visible that the warm Agulhas Current is separated by a more or less narrow band of cold water from the coast in the whole region from Durban to St. Helena Bay, with the exception of a small area just off Cape Agulhas. At the surface this situation is mostly masked by the wind current, which carries warm water in the direction of the coast. Sometimes, however, the cold water ascends to the very surface. This will occur only, when the winds towards the coast, and with that the wind current, are feeble (DIETRICH, 1935*a*, p. 57). Secondly it occurs according to this author when the velocity of the Agulhas Current is greater than usual (especially in the southern summer), for a greater velocity of the current results in a more oblique direction of the isopyknes and, therefore, of the isothermes, and with that in "upwelling" along the coast. The cold water observed sometimes near the coast, therefore, must not be explained by a prevalence of the cold Benguella Current, but by cold "upwelling" water, for these low temperatures exist near shore only, whereas more offshore the higher temperatures of the Agulhas water are to be met with (DIETRICH, 1935*b*, p. 386).

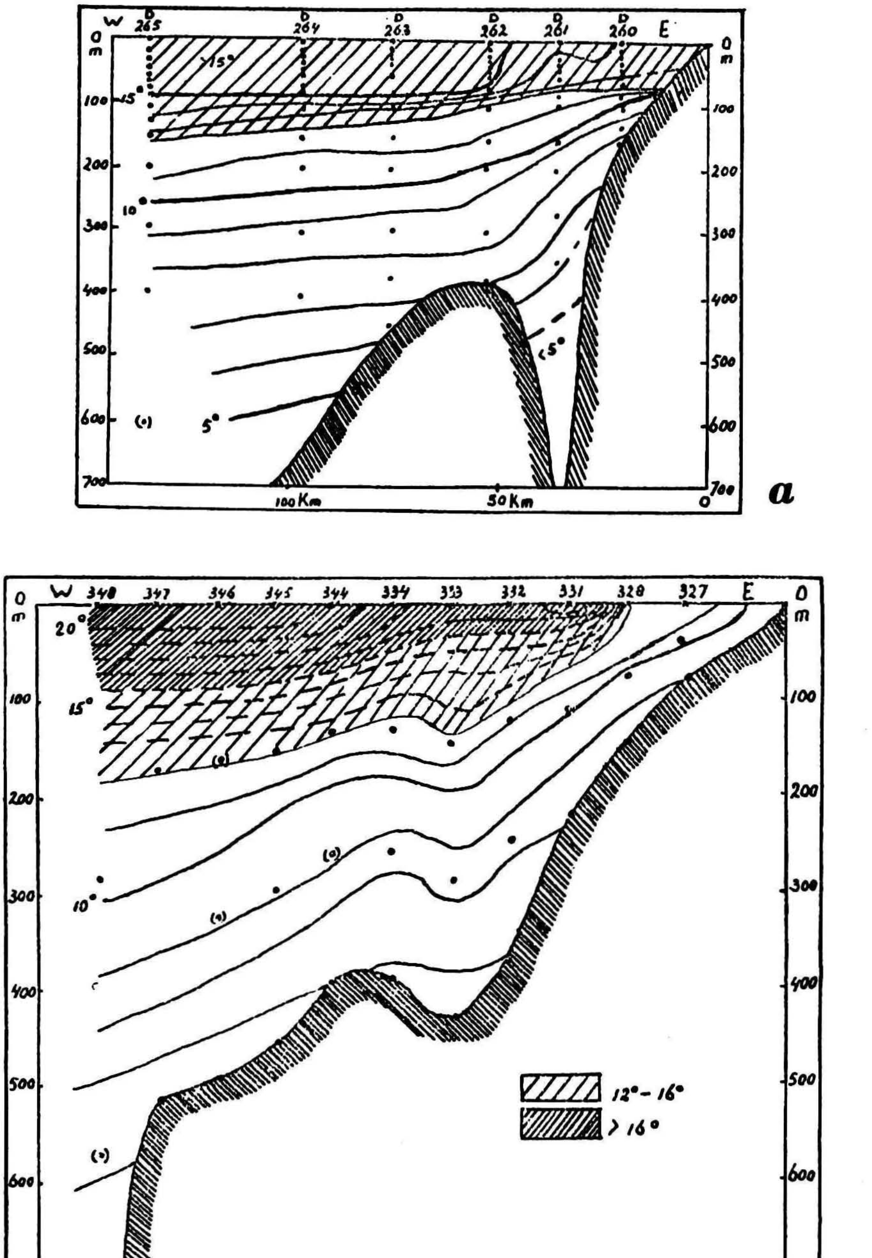

Fig. 6.

Temperature distribution in the Agulhas Current near Saldanha Bay.

a. Profile taken by "Discovery" in the southern winter, 19—20th Juy 1927, from Saldanha Bay to 16° 32′ E, at 33° 6′ S.

b. Profile taken by "Africana" in the southern summer, 9th January—14th February 1933, from Saldanha Bay to 16° 51′ E, at 33° 5′ S.

(After DIETRICH, 1935b, figs. 4 and 5.)

12. SOUTHERN COAST OF FLORIDA.

A similar situation occurs in the Straits of Florida (DIETRICH, 1936, 1937). As is to be expected in the Northern Hemisphere the heavy and cold water occurs on the left hand side of an observer looking in the direction of flow and, therefore, along the coast of S Florida. Usually the cold water does not reach the very surface; this will occur only occasionally: „Die obere Querzirkulation führt das warme Wasser an die Küste von Florida und hindert den dynamischen Auftrieb des kalten und schweren Wassers, bis an die Oberfläche durchzugreifen. Doch Störungen verschiedenen Ursprungs können auch diese Erscheinung, wenigstens in der Nähe der Küste von Florida, verwischen. Wahrscheinlich kann bei starken Pulsationen im Floridastrom die Auftriebszone bis an die Oberfläche durchstossen. Andererseits besitzt die Windverteilung, wie Ch. F. Brooks an den Thermogrammen zwischen Habana auf Kuba und Key West auf Florida gezeigt hat, merklichen Einfluss." (DIETRICH, 1937, p. 68).

CHAPTER V.

The paleontological significance of mass mortality.

In the course of time the paleontological significance of mass mortality has been emphasized, mostly to be refuted afterwards with even more stress. This significance was brought forward in connection with the following problems:

I. In the first half of the nineteenth century mass mortality played an important part in Cuvier's "theory of cataclysms or catastrophes" (CUVIER, 1825). After some decennia, however, this hypothesis no longer found adherents, and with that the interest disappeared in a catastrophe causing mass mortality.

II. Peculiarities of fossils or of their layers.

Every now and then in the history of paleontology some investigators turn up favoring the hypothesis that the fossils of a special deposit did not die in a normal way, but that they perished by accidents or catastrophic events. Peculiarities leading to such a conclusion are for instance a high percentage of young individuals, the presence of females with young, the occurrence of a large number of individuals on a single slab, etc. According to WEIGELT a great part of fossil vertebrates did not die in a normal way. WEIGELT (1927, p. 27) remarks in this respect: Not every fossil bone is the remainder of an animal that perished in an abnormal way, but the vertebrates of which the well preserved remains form rich depsits, certainly died in this way.

As such mortalities cover a restricted area only, it is improbable, that species or even genera were totally exterminated by them, as was surmised in CUVIER's "theory" of catastrophes. WEIGELT's hypothesis surely must not be rejected; however, convincing arguments in favor of this hypothesis are furnished on rare occasions only.

Fossils generally do not occur in one stratum only, but in several strata one above the other. Therefore, it will be evident, that if the animals occurring in a deposit died by mass mortality, this phenomenon must have occurred repeatedly in the same place. Therefore, if it is worth while for paleontologists to study mass mortality occurring in recent times, this pertains particularly to those cases that occur periodically or episodically in the same place.

III. Phosphate concretions.

MURRAY (1890, p. 481; see also MURRAY & RENARD, 1891, p. 397) has proposed the hypothesis that phosphate concretions are formed in places, where great destructions of pelagic animals occur. This hypothesis is taken over by many authors and still finds some adherents in recent time (COLLET, 1908, p. 19; 1932, p. 56; MURRAY & PHILIPPI, 1908, p. 185; GRUTTERINK, 1946, p. 32, etc.). With this subject I shall deal more explicitly in a separate paper.

IV. Origin of petroleum.

The hypotheses on the origin of petroleum may be divided into two groups: the inorganic and the organic, of which the latter is nowadays generally accepted (MACOVEI, 1938, p. 44). In early hypotheses rather large organisms were supposed to be the source material; authors were at variance, however, as to the nature of these organisms, plants or animals being the inducement for much discussion. Amongst the latter widely different groups of aquatic animals were mentioned as source material (HÖFER, 1888, p. 115). To explain the great quantity of petroleum a mass mortality of these organisms seemed to be of importance. As the source beds of petroleum became more and more known, it turned out that most of these groups are strikingly scarce in them; the fossils found being chiefly plankton organisms and further fishes, crustaceans, insects and macroscopic plants. The microscopic plankton organisms, being according to the present conception the chief source of petroleum, are very short living; therefore, a catastrophe causing a mass mortality of plankton is wholly superfluous for explaining the great quantity of material. The total annual production of the plankton gives much more organic material than a catastrophe of the plankton at one moment (KRECJI, 1936*a*, p. 115). Therefore, in modern petroleum literature the importance of mass mortality is denied with great stress. Nowadays the search is not for an abnormal death of petroleum producing organisms, but for an abnormal preservation of the organic compounds after death; the decay taking place under anaerobic instead of under aerobic conditions.

It is, however, a remarkable fact that fish remains occur frequently in bituminous shales. This occurs in fresh water deposits (e.g., the old tertiary marlshales of the Padang Highlands in Sumatra (SANDERS, 1934), the Green River shales) as well as in marine deposits (Kupferschiefer, etc.; see the various examples given by DEECKE (1913, p. 79; 1920) and MACFARLANE (1923; 1931)). Some of these bituminous fish shales are considered as source beds of petroleum (oligocene menelite shales of the Carpathians, for fish remains in these deposits see PAUCA, 1929*a*, 1929*b*, 1931, 1933*a*, 1933*b*; WEILER, 1933; KRECJI & WEILER, 1928; oligocene of northern Caucasus, for fish remains in these deposits see SMIRNOW, 1932; Californian miocene Monterey shales, for fish remains in these deposits see JORDAN, 1920, 1921, 1925; JORDAN & GILBERT, 1919, 1920, etc.). Consequently several authors arrived at the conclusion that fish (perished by mass mortality) should be considered the only or the chief source of petroleum. In modern petroleum literature, however, this hypothesis finds only few adherents: MACFARLANE (1923; 1931). To prevent confusion I may emphasize that I surely do not agree with the opinion that fishes may form the chief source material. However, I am certainly of the opinion, that a periodical mass mortality occurred at least in some of the places, where source beds of petroleum were deposited, and further that the mass mortalities played some part in connection with the genesis of petroleum, this part being to contribute to the genesis of anaerobic conditions. This opinion is based chiefly on the fact that the sediment occurring in the azoic region near Walvis Bay (and, therefore, at a place where mass mortality occurs periodically) shows a remarkable similarity with the Monterey shales and other source beds.

Being convinced of the paleontological importance of mass mortality WEIGELT (1927; 1930) gives an interesting survey of all cases of mass mortality in recent time, known to him from literature or from personal communication. In search for cases of mass mortality, especially of fishes, I found (besides the records mentioned by WEIGELT) several other records in the literature on recent ichthyology (a long list is given by BASHFORD DEAN, 1923, p. 516); on oceanography; on phytoplankton; on seismology; on geology (see for instance ANDRÉE, 1920; older petroleum literature, etc.); and by personal communications.

WEIGELT (1927; 1930) arranges the records of mass mortality under different headings in order of their cause; the chief causes to which fish mortality is related being death by volcanism, by poisonous gazes (chiefly H_2S) and by an abrupt change in temperature and in salinity of the sea water. Mortality in sea by noxiousness of phytoplankton is not mentioned (WEIGELT, 1927, p. 204, states that in fresh water fish mortality may be caused by waterbloom). Doubting whether the causes of mortality in sea mentioned by WEIGELT and other authors were the true ones, I did not arrange the mortality records in order of their cause, but of their geographical occurrence. In doing so it turned out that various records cited by WEIGELT and other authors under different headings referred to the same place. Therefore, at least a part of the supposed causes is probably incorrect. The Walvis Bay mortality for instance is cited in the papers of WEIGELT (1927; 1930) under 3 different headings: death by volcanism (1930, p. 309), death by gazes (1927, p. 39) and eventually as death by "einer roten Milbe" (1927, p. 203). The mortality near Callao (Peru) is mentioned under death by gazes (1927, p. 39) and under death by changes in the temperature of the sea water (1927, p. 205; independently of this statement on p. 214 WEIGELT refers to the Niño current). As will be set forth below the periodically occurring mortality along the coast of Peru, just as the mortality in the Walvis Bay region, is brought about by noxiousness of red water due to dinoflagellates.

In the second place it struck me that the supposed cause of a mass mortality often has nothing to do with the peculiarities observed. ILG (1902; fide HÖFER, 1902, p. 634) for instance observed a great fish mortality in the southern part of the Red Sea and in the Gulf of Aden. ILG supposed that it was caused by a submarine volcanic eruption. On his inquiry if any volcanic phenomenon had been observed, the answer was negative. Still ILG persevered in the suggestion of the mortality being caused by a volcanic phenomenon and, therefore, it is arranged in paleontological literature (ABEL, 1912, p. 39; WEIGELT, 1927, p. 37) under death by volcanism. The observation made by ILG, that the water had a brownred colour, is, however, not used for explaining the mortality, and therefore, in modern literature this observation is no longer recorded. The only author, who interpreted the brown colour, was HÖFER (1909, p. 95), supposing (very probably correctly) that the mortality was caused by red water of dinoflagellates.

From these few examples, to which others will be added below (see SW coast of India; Florida coast (Everglades hypothesis), etc.), it will be apparent that many cases of mass mortality are not correctly interpreted in literature, several of them being erroneously ascribed to volcanism, to the poisonous H_2S or to a sudden change in the salinity or the temperature of the sea water. As will be set forth below, many cases of mass mortality (probably by far the greater part) have to be ascribed to a cause until now practically not considered in paleontological literature, that is to noxiousness of phytoplankton. The great importance of these cases is that they occur repeatedly (periodically or episodically) in the same place.

CHAPTER VI.

Records of mass mortality caused by noxiousness of plankton.

Phytoplankton is the primary food supply of the sea, all kinds of animals feeding directly or indirectly on phytoplankton. Thus it is normally of great benefit to invertebrates and to fish. There are, however, cases known in which phytoplankton is not to advantage of these animals, but that on the contrary it is very noxious, causing a great destruction among them. This may occur if certain elements of the plankton occur in very dense populations; the number of individuals being so enormous as to discolour the water. If one or a few species of plankton organisms multiply to such a degree as to discolour the water, mostly to the virtual exclusion of all other organisms, one speaks of a waterbloom. (Strictly speaking the name waterbloom should be used for such discolorations only, in which the algae are lighter than water, so that they float on the surface; NAUMANN, 1931, p. 616).

Records of mass mortality caused by waterbloom are known from fresh water, from brackish water and from the sea. Mass mortality may occur with a waterbloom of blue algae, of flagellates and of dinoflagellates. ALLEN (1934, p. 176; see also MURPHY, 1936, p. 279) supposes that mass mortality may be caused by dense populations of diatoms too. This supposition was based chiefly on the opinion of English fishermen of the North Sea (BULLEN, 1908), that it is not worth while to fish for herring, where the water is stinking, the smell originating from large amounts of phytoplankton. SAVAGE & HARDY (1935) and SAVAGE & WIMPENNY (1936) have demonstrated that the herring indeed avoids the large amounts of phytoplankton occurring in a certain time of the year in the North Sea and consisting chiefly of a flagellate, *Phaeocystis* or of diatoms. Very dense populations of phytoplankton (e.g., of diatoms) appear to be avoided by fish and by zooplankton (FISH, 1926; HARDY & GUNTHER, 1935, p. 279; HARDY, 1936). I doubt, however, if diatoms ever cause mass mortality of fish or of invertebrates: at least I never found a definite record of it.

No attempt will be made to give a complete list of mortality records from fresh or from brackish water. A few instances are mentioned only to enable a comparison with corresponding phenomena in the sea.

1. MORTALITY IN FRESH WATER.

In fresh water waterbloom of blue algae is most common (NAUMANN, 1922, p. 665; FRITSCH, 1936, p. 114), waterbloom of dinoflagellates being rather rare (NAUMANN, l.c., p. 679). Therefore, it is not surprising that most cases of mortality in fresh water occur in connection with a waterbloom of blue algae. LINDEMANN (1926, p. 117) remarks that on the rare occasions of a mass development of dinoflagellates in fresh water they may be also noxious to fish. (For the hypothesis that waterbloom should be only indirectly noxious, see chapter VII.)

Mass mortality of fish in connection with waterbloom in fresh water is mentioned by COHN (fide LAMPERT, 1899, p. 513; 1925, p. 590); KAFKA (fide STRODTMANN, 1898); SEYDEL, 1913; REDEKE, 1916; VAN GOOR, 1920; NIENBURG, 1924, p. 104; NAUMANN, 1922, p. 665; WEIGELT, 1927, p. 204, etc.). According to WEIGELT a waterbloom occurs in West Texas and many other countries at a low water level of the rivers, giving rise to a mass mortality of fish. COHN mentions that a waterbloom of the blue alga *Anabaena circinalis* Rabenhorst in a lake near the village of Zirke in Posen caused fish mortality.

The noxious effect of blue algae is furthermore shown by the fact that cattle and fowl may die within a very short time after drinking water with waterbloom of blue algae. Such records are known from the lakes forming the estuary of the Murray river, southern Australia (FRANCIS, 1878); from several lakes in Minnesota (ARTHUR, 1882; PORTER, 1886; NELSON, 1903; FITCH et al., 1934); and also from Fort Saskatchewan, Alberta, Canada (GILLAM, 1925); S. Dakota (FITCH et al., l.c.); Lake Vesijärvi, Finland (FITCH et al., l.c.).

The oldest record of fish mortality in discoloured water is that mentioned in the Bible as one of the seven plagues of Egypt "and all the waters that were in the river were turned to blood. And the fish that was in the river died; and the river stank, and the Egyptians could not drink of the water of the river; and there was blood throughout all the land of Egypt." (Exodus, VII, 20, 21). A mass development of phytoplankton occurs annually in the river Nile in the last week of June; the colour usually being green and consisting of different groups of phytoplankton organisms. During that time (2—2½ weeks) the water of the Nile is evil smelling and undrinkable (KAUFMANN, 1897; STEUER, 1911, p. 357; BRUNNTHALER, 1914). In the Mosaic account the phytoplankton was probably rather monotonous in composition due to an unusual mass development of one or a few species.

2. MORTALITY IN BRACKISH WATER.

In brackish water fish mortality may occur in connection with a mass development of blue algae, of flagellates and of dinoflagellates.

BLUE ALGAE.

Waterbloom of blue algae is rather common at some places in the Baltic (SJÖSTEDT, 1922), especially in semiseparated parts as the Baltic lagoons (Kurisches Haff; Stettiner Haff, etc.). This so called "Haffblüte" occurs annually and in severe cases may bring about great mortality of fish (ANONYMOUS, 1896; SCHIEMENZ in: SEYDEL, 1913, p. 90). Before the endikement of the Dutch Zuiderzee waterbloom of blue algae did not occur (REDEKE, DE LINT, VAN GOOR, 1924, p. 100); some years after the endikement when the salinity had much decreased, a heavy waterbloom of the blue alga *Aphanizomenon flos aquae* Ralfs., the so called green water of Urk, was observed causing a great destruction amongst fish (1941); moreover, near the shore frogs and newts were found dead too (KRISTENSEN, 1943, and in litt.). Since that year the waterbloom occurs every summer in a more or less pronounced degree. Mortality occurs only during heavy occurrences of waterbloom.

FLAGELLATES.

LIEBERT & DEERNS (1920) attributed an extensive fish mortality occurring in the brackish water of the Workumer Nieuwland Polder (a diked marsh in the Netherlands) in March 1920 to noxiousness of a flagellate with green pigment. The authors only denominate this flagellate "Chrysomonadine van Workum"; according to OTTERSTRØM & STEEMANN NIELSEN (1940, p. 18) the species is *Prymnesium parvum* Carter, 1938. OTTERSTRØM & STEEMANN NIELSEN (l.c.) ascribed cases of extensive fish mortality in two Danish brackish water lakes to noxiousness of the same flagellate species: in the Ketting Nor it occurred in September 1938 and in the Selsø Sø in the latter half of September 1939; in the last named lake a similar mortality had been observed already previously (1933).

DINOFLAGELLATES.

LINDEMANN (1924; 1926) attributed a great fish mortality in the harbour of Rostock (Baltic coast of Germany) in October 1917 to a yellowish waterbloom of two species of dinoflagellates, *Heterocapsa triquetra* (Ehrenb.) Stein and *Glenodinium foliaceum* Stein.

3. MORTALITY IN SEA.

In sea fish mortality may occur with a mass development of flagellates and of dinoflagellates; until now only a few, rather insignificant cases are known to me of mortality in sea occurring in water with waterbloom of blue algae.

Mortality in sea caused by BLUE ALGAE.

A survey of the older literature of waterbloom in sea caused bij blue algae is given by WILLE (1904). It occurs especially in warm seas (chiefly species of the genus *Trichodesmium*). Following warm currents it may occur in relatively high latitudes: Kuro Shio; Brazil Current at the Atlantic coast of South America. In the latter current especially from 10° S to the mouth of the La Plata waterbloom of *Trichodesmium* occurs very frequently; a great many records of discoloured water (mostly yellow) in this region are given by HALTERMANN (1898); the most southern record is that given by HART (1934*b*, p. 174), who observed waterbloom of

Trichodesmium thiebautii Gomont at 40° S. For red water caused by blue algae in the Red Sea see p. 60.

From the above mentioned instances it will be obvious that waterbloom of *Trichodesmium* species is a rather frequently occurring phenomenon. Of mortality in *Trichodesmium* waterbloom, however, only a few, rather insignificant cases are known to me. As blue algae may cause great mortality in fresh and in brackish water, the possibility is not excluded that more records of mortality in sea caused by blue algae waterbloom will become known in future. Waterbloom of *Trichodesmium* floats on the surface of the water and, therefore, most fishes will be able to avoid it in the open sea. It seems, however, possible that fish mortality occurs in very severe cases of this waterbloom occurring in shallow water near the coast, where escape is impossible. The following records of noxiousness of blue algae in sea are known to me: According to native fishermen of the East Indian Archipelago fish get stunned in a mass of *Trichodesmium* (VEENHUYZEN, 1879): VEENHUYZEN himself often observed a small species of fish floating as if intoxicated on the surface of the water in places where *Trichodesmium* was abundant.

In October 1940, after a very dry season *Trichodesmium* approached the shore at Balikpapan (east coast of Borneo) (normally it is found farther offshore, avoiding the brackish water near the coast; vide DELSMAN, 1939, p. 155). Mortality was observed in the little pools on the beach among fishes, crustaceans, worms (*Nereis* species), etc. Mortality was observed also in the outlets of many rivulets (MOHLER, 1941).

It remains to be ascertained if the mortality occurring in some years at Kamaran (Red Sea) (see p. 60) and that near the coast of Ceylon (see p. 64) are caused by blue algae or by dinoflagellates.

Red water of *Trichodesmium* was frequently observed by the Great Barrier Reef Expedition near Low Isles (YONGE, 1930, p. 122). Prof. C. M. YONGE (in litt.) kindly informs me that no mortality was observed.

THE PHENOMENON OF RED WATER.

In sea waterbloom of dinoflagellates, so called red water, occurs in some regions rather frequently, contrary to fresh water, where this waterbloom is a rare phenomenon (NAUMANN, 1922, p. 679). It is, therefore, not surprising that by far the greater number cases of mortality in sea occur in red water of dinoflagellates; further mass mortality is known to occur with certainty in water coloured a reddish amber by flagellates.

As red water of dinoflagellates is the chief cause of most of the periodically and episodically occurring mass mortalities in sea and very probably played a part at the origin of some bituminous shales, some remarks will be made on these organisms and on the phenomenon of red water.

Dinoflagellates are unicellular plankton organisms, some being armoured with plates of cellulose, others being unarmoured or naked. Owing to the destructibility of these plates they are usually not preserved in bottom deposits; still there are several species described from fossil deposits (DEFLANDRE, 1935). A large number of dinoflagellates are holophytic and, therefore, the group is mostly treated under phytoplankton; others are holozoic (*Noctiluca* for instance) or saprophytic in their nutritional requirements. They are very important with regard to the food supply of the sea, coming second only to the diatoms. All are microscopic, ranging in size from 7 μ to 2 mm, which is the size only occasionally reached by *Noctiluca*, the largest known dinoflagellate (LEBOUR, 1925, p. 2). By most authors the genus *Noctiluca* has been placed with the dinoflagellates, as has been done in this paper too; by other authors it has been referred to a separate group, the Cystoflagellata.

Dinoflagellates are one of the common causes of phosphorescence (= luminescence) of the sea. Luminescence is not a very reliable indication, that the dinoflagellates are present in huge masses. They may give already a startling display of light if present in relatively small numbers. The occurrence of red water, however, is a sure indication of very high abundance (ALLEN, 1941, p. 612).

During red water outbreaks the dinoflagellates multiply with great rapidity (NIGHTINGALE, 1936). By this rapid increase in number the sea may become suddenly a deep red or chocolate colour (LEBOUR, 1928). These plankton swarms are to a very large extent exclusive against other organisms in their particular area, many of which in fact are killed (ALLEN, 1941, p. 611); therefore, the plankton in these swarms is very monotonous in composition. The following remark by ALLEN (1942) will give an idea of the number of individuals that must be present to cause a distinct red colour: "Even an experienced observer may sail through an expanse of water showing a dingy chocolate or other inconspicuous color and think nothing of it, although the microscopic organisms causing the color may be present in numbers of a half million to a full million per liter of sea water near the surface. Yet the difference between that color and one of distinct redness may rest only on the presence of another million or two, a mere doubling or trebbling of the less conspicuous density of population." This remark gives an explanation of the fact that red water may appear and disappear rather suddenly for a mere doubling or a mere halving of the number may be sufficient to make the colour striking or inconspicuous.

"Red water may remain in a given area for varying periods of time, in some instances between tidal intervals only, and in others for days or weeks" (NIGHTINGALE, 1936). According to LEBOUR (1928, p. 130) the red colour is caused by enormous masses of dinoflagellates with brown or orange yellow chromatophores. MARTIN & NELSON (1929) suggest, however, that the colour is due to the reddish fluorescence of chlorophyll present in very great quantities. With regard to the fact that the cells hold together in dense masses MARTIN & NELSON remark that the cells are surrounded by a gelatinous envelope, "so that the water in which they occurred must have been a nearly continuous mass of soft jelly" (observed on red water of a *Gymnodinium* spec.). HORNELL & RAMASWAMI NAYUDU (1924) made the following observation on "red water" of flagellates (Flagellate "B") at the Malabar coast (see below): When a sample of water with "waterbloom" of this flagellate was allowed to stand for a little while, the organisms settled rapidly to the bottom where they formed a gelatinous deposit of considerable bulk. "In this jelly like mass derived from the swelling up and coalescence of the colourless limiting membrane of cortex of each individual, they are seen to be embedded, more or less rounded in form, inactive and without a trace of a flagellum." "On one occasion (27th September 1922), when the sea was absolutely smooth and motionless, the bottom at a depth of two or three feet was seen to be covered with a deep layer of similar consistency and colour." A similar observation was made with dinoflagellates (*Glenodinium* spec.) at the Malabar coast, when present in great abundance. When left in undisturbed water they formed a gelatinous mass upon the bottom.

Mortality in sea caused by red water of flagellates: SW COAST OF INDIA (Malabar and South Kanara coasts).

Mortality caused by flagellates occurs annually at the Malabar and South Kanara coasts. According to HORNELL (1917) red water of dinoflagellates and of flagellates both occur rather frequently on this coast; mortality was observed by HORNELL in the flagellate water only. (Apparently during the years of observation injurious species of dinoflagellates never were present in such huge masses as to cause mortality). The characteristic names for the discoloured water are: Karanir (shore water), Sennir (red water) and Kedunir (bad water).

The following data, on which mortality and/or "red water" (in fact the colour is often olive brown) were observed, are known to me:

1507, 25? August: Great mortality of crabs and prawns at Cannanore. The number of the dead animals must have been very considerable as will be obvious from the following: The Portuguese were besieged at that time in Cannanore and nearly died from starvation but as the sea sent forth shoals of crabs and prawns, the garrison again lived in plenty, HORNELL, 1917, p. 65; ANONYMOUS, 1933, p. 253.

1861, 1 November: Fish mortality between Mangalore and Cannanore. DENISON, 1862, p. 453; ANONYMOUS, 1862, p. 320.

1871, end of October to early in November: Fish mortality at Mahé. JOUAN, 1875, p. 23.

1908, November: Excessively great mortality off the Mangalore coast affecting even large shoals of sardines. HORNELL, 1917, p. 53.

In 1916 the phenomenon was studied by HORNELL (1917) who made the following observations of red water and of mortality:

1916, last week of August: red water at Cannanore and mortality of crabs and soles.

1916, 20 September: bright patches a mile offshore consisting of a nearly pure gathering of *Noctiluca*. No mortality.

1916, 25 September: "karanir" and mortality of fish and crabs (chiefly *Neptunus pelagicus*) at Cannanore. The karanir disappeared with a sudden change of the weather.

1916, early in October: olive-brown water swarming with flagellates. Mortality at Cannanore among fishes, crustaceans, molluscs and Alcyonaria. The mortality lasted for three days. On the 4th day it decreased markedly; the number of the flagellates having sensibly decreased coinciding with a change of the weather.

1916, 9—15 October: Flagellate water at Calicut accompanied by fish and crab mortality.

1922, early in the "season": baskets of dead and dying sardines and other fish were washed ashore at Chaliyam (7 miles south of Calicut): HORNELL & RAMASWAMI NAYUDU, 1924, p. 142.

1922, 22 September: Flagellate water caused mortality at Calicut. HORNELL & RAMASWAMI NAYUDU, 1914, p. 142.

This list gives a very incomplete impression of the frequency of the phenomenon. According to HORNELL (1917) "red water" and mortality occur annually along certain stretches of the coast, although the extent of the phenomenon may vary within wide limits. In several years the mortality is only local in occurrence and affects only a few species close inshore. In other years, however, many and diverse kinds are involved, and it may affect large shoals both close inshore and at several miles from the coast. Very great mortalities occur in some years only.

The mortality was attributed by DENISON (1862, p. 453; see further ANONYMOUS, 1862, p. 320; JONES, 1882; GEIKIE, 1893, p. 648) to a sudden change in the salinity of the sea water. The following statement by STUTZER (1931, p. 309) is probably based on DENISON's opinion: „An der Küste Indiens ... erfolgt durch ins Meer eintretende Süsswasserfluten oft ein Massensterben der Meeresorganismen". JOUAN (1875) describing the same phenomenon does not give an explanation as to its cause. A very exact description of the occurrence is given by HORNELL (1917) and HORNELL & RAMASWAMI NAYUDU (1924). According to HORNELL (1917) the mortality is caused by a Euglenid flagellate; this flagellate is denominated by HORNELL & RAMASWAMI NAYUDU (1924, p. 140) as "Flagellate B". The colour of the water with Flagellate B is described by HORNELL (1917) as olive brown; according to HORNELL & RAMASWAMI NAYUDU (1924, p. 140) Flagellate B when occurring in multitudes imparts a distinct reddish amber tint to the water.

Red water and mortality occur in a certain season only: from the last week of August to the beginning of November.

The organisms found dead by HORNELL near Cannanore in 1916 are the following [1]):

I. Fishes: chiefly soles (*Plagusia bilineata*), small jewfishes (Sciaenidae) together with smaller numbers of catfishes, nonthal (*Sillago*) and Koruppan (*Platycephalus*).

II. Crustaceans: many crabs, chiefly *Neptunus pelagicus*, with a few *Thalamita, Scylla, Neptunus sanguinolentus* and *Matuta*; crayfishes (*Palinurus*); thousands of specimens of *Hippa*, further *Albunea* and small hermit crabs.

III. Molluscs were also greatly affected: *Donax cuneata* being found dead in great quantity, further a small *Pholas*, some Mytilids, *Donax scortum*, a large *Mactra* and other bivalves.

IV. Alcyonaria: Many specimens of *Cavernularia*.

The sardines are seldom affected in any quantity, as they are generally careful to avoid entering the poisonous water; on those rare occasions of excessively great mortality, however, the sardines are affected too, the sea being covered for miles with enormous multitudes of dead sardines. Such an enormous mortality occurred in 1908; the area affected being over fifteen miles in length and extending generally from one to two miles offshore. From this statement it is apparent that the poisonous water may occur in the open sea some miles offshore; the most favourable conditions for severe concentrations of poisonous water, however, seem to prevail in the sheltered water of embayments (HORNELL, 1917, p. 59).

Mortality in sea caused by red water of dinoflagellates: I. SW AFRICA.

The mortality occurring annually in a certain season in Walvis Bay and in other places along the coast of SW Africa is attributed in this paper to red water of dinoflagellates. The red colour of the water examined by MARCHAND (1928) was due to a dinoflagellate of the genus *Noctiluca*. By a future study of the plankton it will have to be ascertained whether the red colour of the water (in which mortality occurs) is always caused by *Noctiluca*, or that (what is most probable) other dinoflagellates may be also responsible.

The fact that the mortality in one year is much greater than in another, is according to CLASSEN (1930) wholly due to accompanying circumstances: in the first place to the direction of the wind, that pushes the dead fishes either to the land or to the open sea. In the second place CLASSEN points to the hypothesis put forward already by SCHULTZE (1907) that the catastrophe will be great, if it occurs at the time when the sardines or other migratory fish have entered the bay. Although these factors surely are of importance, the extent of the mortality in my opinion does not depend wholly and even not chiefly on accompanying circumstances. It will depend chiefly on the fact whether the circumstances are favourable for great outbreaks of red water. In some years in which a very favourable combination is present of the factors needed for outbreaks of red water, the latter will be very heavy and will occur over vast areas and with that the mortality will be exceedingly great (see further chapter IX).

It is possible, although surely not certain that great outbreaks of red water and with that great mortalities occur at the coast of Peru particularly in false-Niño years (see p. 51). Therefore, the question must be answered whether the great mortalities near Walvis Bay occur in years of meteorological disturbances too. Possibly there is some relation between the years in which the Kuiseb "comes down" and the years of great mortality (cf. p. 27 and p. 10); both perhaps being the result of the same meteorological conditions. A very great mortality occurred near Walvis Bay in the southern summer of 1924/1925 and, therefore, in a year of false Niño disturbances at the coast of Peru. As far as I am aware, however, great meteorological disturbances occurred at the coast of SW Africa only in 1893 and 1933/1934. Records of an abnormally great mortality in those years are unknown. Therefore, there seems to be no relation between these very abnormal years and the occurrence of an abnormally great mortality along the coast of SW Africa. Until now the records are, however, much too scarce to draw any definite conclusions.

Mortality in sea caused by red water of dinoflagellates: II. SOUTHERN CALIFORNIA (Santa Barbara to San Diego).

Although red water and mass mortality occur in this region on rather rare occasions only, it will be treated of first, because the phenomenon of red water has been investigated thoroughly. Qualitatively the plankton has been studied since several decennia (TORREY, 1902; KOFOID, 1911; KOFOID & SWEZY, 1921, etc.). Quantitative studies were begun on material obtained in 1917; since 1919 daily catches recorded in numbers per liter are made at the Pier of the Scripps Institution on La Jolla Bay, and since 1920 also at Pt. Hueneme (near Oxnard). Moreover, a number of catches were made at other inshore stations and offshore positions. The results of this research are given in several papers by ALLEN (1921*a*, 1921*b*, 1921*c*, 1928, 1929, 1933, 1935, 1938, 1941, 1942, 1946*a*, 1946*b*), CUPP (1943), etc. Since 1901 special interest was paid to the phenomenon of red water. Extensive areas of red water occur by no means frequently. The records mentioned below will not cover all the occurrences of red water in Southern California since 1901; the very thorough investigations of the Scripps Institution warrant, however, that they give a fairly good impression of the rarity of conspicuous occurrences.

Red water occurs in bays as well as in the littoral part of the sea; according to ALLEN (1941, p. 633) no red water has been observed in Southern California waters farther than thirty miles offshore.

The following records of conspicuous occurrences of red water and/or of mass mortality are known:

1894, end of February: great fish mortality between San Diego and Santa Barbara; dead animals chiefly observed on the Santa Monica and the Redondo Beach. Dead fishes were observed for the first time on 24—II: thousands were found dead on 28—II. A yellow slime was observed on the gills of the fish. The fish found dead by TANNER (1896) on the Redondo Beach were barracuda, flatfish, sardines, anchovies, etc. To explain this mortality TANNER supposes that some seismic disturbance caused submarine oil springs to burst forth throwing out an unusual amount of oil and gas. Although happening rather early in the year the possibility does not appear to be excluded, that the mortality was caused by noxiousness of dinoflagellates just as the records described below from the same region. In the summer of the same year apparently mortality occurred again, for PECKHAM (1897; see further HÖFER, 1909, p. 94) mentions a great mortality in summer between Point Conception and Ventura over a distance of at least 200 miles.

1901, mid July: Red water with an accompanying mortality of fish and invertebrates was observed by TORREY (1902). In dinoflagellate literature this is the oldest known record.The red water consisted chiefly of the dinoflagellate *Gonyaulax polyhedra* Stein. "None of the following cases are at all comparable in extent and visible influence with the red water of 1901 lethal in mid July over two hundred miles of coast line from San Diego to Santa Barbara and visible near San Diego as late as September 1". (KOFOID & SWEZY, 1921, p. 354). On the first day of the mortality chiefly fishes, squids and holothurians (*Trachostoma arenata*) were thrown up; the fishes and the squids were dead, but many of the *Trachostoma* lived for several days. The dead fish consisted nearly exclusively of benthonic living forms. Most of them were Selachii: *Myliobatis californicus, Urolophus halleri, Rhinobates productus, Platyrhinoides triseriatus, Gyropleurodus francisci, Galeus californicus;* further a red perch, a large numbre of smelts and the blind fish *Typhlogobius californicus.* After some days many crustaceans came ashore, viz., many crabs: *Tevila crassatelloides, Petrolisthes cinctipes, Cancer antennarius.* Finally great numbers of *Hippa analoga* were thrown up; most of them alive but apparently debilitated and unable to dig as is their habit. They were mostly of large size.

1907, early part of August: Red water occurred along a great part of the coast of Southern California at least from San Diego to San Pedro (ca. 100 miles) consisting of *Gonyaulax polyhedra* Stein. It caused mass mortality among fishes and invertebrates (see photograph of the dead animals on the shore at East San Pedro in KOFOID, 1911, p. 244, fig. E).

1917, 4 June: Red water was observed 12 miles west of San Pedro consisting of *Prorocentrum micans* Ehr.; no injury was observed (ALLEN, 1921b).

1917, September: Red water consisting mainly of *Gonyaulax polyhedra* Stein occurred close inshore near Santa Barbara causing a good deal of injury to fish and to the shore fauna (ALLEN, 1921b, p. 543).

1924, June: Red water consisting chiefly of *Prorocentrum micans* Ehr. became visible on June 1 for nearly two weeks at La Jolla Bay. On June 16 "stinking water" had become prominent. June 3 ten miles offshore from the La Jolla Pier "yellow water" was reported, the lighter colour probably being due to a lesser density of the organisms. The colour of the water in La Jolla Bay was mostly brownish or dull brick red, also yellowish in thinner spots. The number of individuals was June 1 near the bottom 55000 ex. per liter and near the surface 35000 ex. per liter. No damage to the fauna was observed; fish swam through the red water with apparent indifference (ALLEN, 1928).

1933, 17 to 31 May: Red water was observed around the shores of La Jolla Bay consisting chiefly of *Prorocentrum micans* Ehr. "On several of the fourteen days of occurrence the discoloration appeared to be nearly uniform in a zone of water within a half mile off shore over a distance of at least three miles arround the shores of La Jolla Bay. On other days it appeared streaky, probably due in part to more wind disturbance." No damage to the shore fauna was observed: "Fish seemed to act much as usual in this water" (ALLEN, 1933).

1938, end of May to early in June: Red water consisting chiefly of *Gonyaulax polyhedra* Stein was observed at La Jolla. On June 7 red water occurred also off San Diego; the area affected being probably 25 to 30 miles long and 5 to 10 miles wide. On June 3, the abundance of *Gonyaulax polyhedra* being 500.000 individuals per liter, the colour of the water was a dingy or muddy chocolate; on June 6, when the colour was much like that of fresh blood, the number of *Gonyaulax* specimens was about 3 million ex. per liter. No damage to the shore fauna was observed (ALLEN, 1938, p. 55).

1939: Red water near La Jolla Bay consisting chiefly of *Prorocentrum micans* Ehr. No damage (ALLEN, 1941, p. 627; 1942).

1945, September—October: Red water near La Jolla Bay consisting chiefly of *Gonyaulax polyhedra* Stein; the number of individuals amounting in one of the catches to more than 6 million per liter. No damage to the shore fauna was observed (ALLEN, 1946a; 1946b).

From these records it will be obvious, that red water and mortality occur most often in summer. The animals found dead are fishes as well as invertebrates. Not all organisms are equally affected; in the first place bottom living forms, such as bottom living fish, squids, holothurians and littoral crustaceans, such as *Hippa analoga* and *Cancer antennarius* (KOFOID, 1911, p. 243).

In this region it has been understood as early as 1901 (TORREY, 1902) that the destruction of great numbers of fish and invertebrates occurring in some years on this coast is caused by red water of dinoflagellates. Outbreaks of red water are, however, rather rare (1901, 1907, 1917, 1924, 1933, 1938, 1939); and the destruction of fish, etc. is even more rare. Since the beginning of the researches of the Scripps Institution only two species of dinoflagellates, *Prorocentrum micans* Ehr. and *Gonyaulax polyhedra* Stein, ever became so excessively abundant as to cause red water (ALLEN, 1941, p. 633). During the three red water occurrences of *Prorocentrum micans* (1924, 1933, and 1939) the fish and invertebrate fauna were not affected. As yet only red water consisting of *Gonyaulax polyhedra* produced lethal effects. In 1938 and 1945, however, red water of this species was not injurious; the reason why is not settled.

Mortality in sea caused by red water of dinoflagellates: III. WASHINGTON STATE (Olympia Oyster region).

Red water in which *Gymnodinium splendens* Lebour is mostly predominant occurs repeatedly in this region (NIGHTINGALE, 1936). Sometimes it causes some mortality among oysters, especially among young oysters. The mortality is apparently not considerable. The phenomenon of red water was observed by NIGHTINGALE in Oakland Bay in the summer of 1929, 1934 and 1935. In 1936 an extensive study of red water was made by NIGHTINGALE in the whole Olympia oyster region. He listed 21 occurrences of red water, ranging from a few hundred to several thousand square yards in extent.

Mortality in sea caused by red water of dinoflagellates: IV. PERU.

Red water of dinoflagellates and accompanying mortality of fishes and invertebrates occur repeatedly along the coast of Peru. These phenomena occur mostly between the end of December and the end of April. Various hypotheses have been put forward as to the cause of the mortality; the chief ones are the following:

1. Volcanism: RUDOLPH (1887, p. 202; 1895, p. 577) attributed the fish mortality in the Bay of Callao on 30–III–1828 with accompanying

evolution of H_2S to the tremendous earthquake occurring at that time in Peru. As in many years mortality occurs in March accompanied by evolution of H_2S, but without volcanic phenomena it seems probable that the 1828 mortality had the same cause as those in other years; this cause being red water of dinoflagellates. FORBES (1858) attributed a mass mortality of crabs in 1857 in the Bay of Payta with an accompanying change in the colour of the water to an earthquake. The number of dead crabs was so great that they were thrown up on the beach in a raised wall-like line, 3 to 4 feet wide, and to the height of about 3 feet, along the whole extent of the bay. According to HUTCHINSON (1873; see also Army and Navy Journal, d.d. 2—9 May 1874; ANONYMOUS, 1874) the repeatedly occurring mortality at the coast of Peru is caused by H_2S, the latter being of volcanic origin.

LAVALLE (1917*a*; 1924) has demonstrated the non volcanic origin of the phenomenon.

HUTCHINSON's hypothesis forms a transition between 1 and 2.

2. H_2S. BURTT (1852; 1854) ascribes the fish mortality in the Bay of Callao to a poisoning by H_2S. This assumption is taken over in paleontological literature: WALTER, 1927, p. 325; WEIGELT, 1927, p. 37; VON KOENIGSWALD, 1930, p. 243, etc.

3. A sudden change in the temperature of the sea water caused by a southward flow of the false-Niño current (for the nature of this current, see p. 30) kills the fishes.

This hypothesis was advanced for the first time by LAVALLE (1917*a*) and is now accepted by most authors; e.g. by WEIGELT, 1927, p. 31 and 213; GUNTHER, 1936*a*, in part; SVERDRUP, JOHNSON, FLEMING, 1946, p. 274, 705.

4. Red water of dinoflagellates. Red water occurs frequently along the coast of Peru. CARILLO (1892) for instance observed on many occasions reddish ochre coloured water at the coast of Peru; according to LAVALLE (1917*a*) the discoloration was caused by dinoflagellates. Opalescent water of a reddish (sometimes dark coffee) colour accompanied by a very intense phosphorescence at night was frequently observed in the Bay of Chorillos (near Callao) during the southern autum by Carranza (fide LAVALLE, 1917*a*). COKER (1910) remarks: "The great red seas, formed sometimes at least, of myriads of microscopic dinoflagellates, are of common occurrence. They are of uncertain value and sometimes seem to work much injury." TAYLOR (1917, p. 14) in mentioning that the mortality of fishes and invertebrates near the Florida coast is possibly due to red water of dinoflagellates continues: "Dr. R. E. COKER records (in unpublished notes) from the coast of Peru a phenomenon possibly due to the same cause." According to STIGLICH (1925; fide GUNTHER, 1936*a*, p. 231) during occurrences of red water besides fishes shrimps, octopuses, other molluscs, sea urchins and various other animals perish in great numbers. GUNTHER

(1936*a*) himself assumes two possibilities: 1° he gives LAVALLE's hypothesis of mortality by abrupt changes in the temperature of the sea water, especially in false-Niño years, and 2° GUNTHER gives strong support for the hypothesis, that mass mortality (occurring in normal years) is brought about by noxiousness of red water.

Although LAVALLE (1917*a*, 1917*b*) did not arrive at a correct interpretation of the direct cause of the fish mortality, he gave an excellent exposition of the phenomenon, that is known in Callao under the local name of aguaje (in Pacasmayo the same phenomenon is called salgaso). According to this author aguaje always begins with, and the general character of aguaje is a reddish ochre (sometimes coffee coloured) discoloration of the sea water caused by dinoflagellates; moreover, the water becomes opalescent on account of the enormous mass in which these gelatinous organisms are present. Aguaje occurs according to LAVALLE (1924, p. 99), when the warm Niño current comes in contact with the cold water of the Peru Coastal Current. During the southward flow of El Niño the aguajes may be observed on the respective places of interference between the cold and the warm currents. GUNTHER (1936*a*, p. 192, 216, 232) emphasizes that the warm wedges converging sometimes with the coast (see p. 30 of the present paper) may produce red water, and therefore, aguaje too. Thus, aguaje does not occur only in the abnormal false-Niño years, but may occur under normal conditions too. Dr. E. SCHWEIGGER (in litt.) made several observations of red water along the coast of Peru. He arrives at the same conclusion as GUNTHER with regard to the circumstances under which it occurs: "red spots occur frequently in all places where warm water invades the cool water of the Peru Coastal Current". If the occurrence of red water is followed by mortality of fishes and invertebrates, it will be obvious that this mortality occurs also in the places where the warm water invades the cool water. This may be the reason why the mortality is often ascribed to sudden changes in the temperature of the sea water. See further p. 67.

GUNTHER will be right to say that mortalities occurring in normal years are brought about by noxiousness of red water. It remains to be investigated whether GUNTHER is right in ascribing the great fish mortalities in false-Niño years to a sudden change in the temperature of the water. These mortalities are perhaps also the result of noxiousness of red water, for it is possible that heavy outbreaks of red water and with that great mortalities occur particularly in false-Niño years. The following remark of SCOTT (in: MURPHY, 1926, p. 36) about the phenomena in the very abnormal year 1891 argues for this supposition: "After dark the sea broke in phosphorescent lightnings all along the coast. During the day it was covered with blood like patches many acres in extent caused by these minute organisms".

Red water may vanish without any evolution of H_2S, see for instance the observation by RAIMONDI (1891, p. 62) on 13–II–1886 at La Punta.

At various occasions, however, the occurrence of red water is followed by an evolution of a great quantity of H_2S. The latter is often so intense, that it blackens silver and the white paintwork of ships lying in the harbours of Peru. Therefore, aguaje is called also El Pintor or Callao Painter. As the emitting of H_2S is a very conspicuous phenomenon, aguaje is synonymized by many authors with an evolution of H_2S. LAVALLE (1917*a*) has, however, emphasized that the general character of aguaje is a reddish discoloration of the sea and the opalescence, whereas the evolution of H_2S occurs only locally. The latter develops only in such places, where a great mass of red water plankton (dying off for a great part shortly after the plankton maximum) is deposited on the sea bottom. LAVALLE emphasizes that the evolution of H_2S occurs only after the death of the plankton. With regard to this fact LAVALLE mentions the observations of HUTCHINSON (1873) made during aguaje: At first the water became opalescent and obtained an ochre brown colour with a reddish tinge; 12 hours later the colour of the water became dark green; again 14 or 16 hours later the colour was muddyish white and the nauseous odour of H_2S was perceptible. As the water assumed the white milky colour, no more organisms were perceptible in the water.

Sea water collected on various spots in the water of the Bay of Callao during aguaje on 28th April 1885 contained according to RAIMONDI (1891, p. 62) a quantity of H_2S varying between 0.00874—0.07431 liter per liter water. A further peculiarity of aguaje are the great spots of thick scum on the water surface, originating after the death of great masses of the fatty plankton (LAVALLE, 1917*a*, p. 328).

Aguaje occurs in various parts of the coast of Peru; apparently it does not occur as far north as Guayaquil (RAIMONDI, 1891) and probably it is rather heavy in the vicinity of Pacasmayo and Eten. Here in some years the mortality is so enormous, that the farmers have to send waggons and people to clear away the rotting fish. At such occasions the development of H_2S is so intense that the odour is even observable at San Pedro, situated at a distance of nearly 8 km. During the Chilean occupation (1881—1884) an enormous mortality caused by aguaje occurred in the vicinity of Eten. The rotting fish were buried by the Chilean soldiers in a trench, stretching from Pimentel to Chiclayo.

RAHM (1937, p. 1246) observed thousands of dead fish in August 1934 in the vicinity of the Chincha islands, the sea having a blood red colour. RAHM supposes that the red colour was due to the red pectoral fins of the fishes; as RAHM travelled by aeroplane it is very probable, that this supposition is incorrect.

A great mortality of birds (LAVALLE, 1917*b*, 1924; MURPHY, 1923; 1926) occurs in some years too on the coast of Peru. The chief cause of the death of the birds is starvation (starvation being either the direct or the indirect cause of death); the lack of food being the result of the departure of the normal food fishes (chiefly anchovies), when water of high temperature invades the cool water of the Peru Coastal Current (LAVALLE, l.c.). This is certainly correct; the possibility is, however, not to be excluded that on some occasions the birds die by eating fish poisoned by red water of dinoflagellates.

Mortality in sea caused by red water of dinoflagellates: V. JAPAN.

Red tide ("Akashiwo") is well known among Japanese fishermen. It occurs repeatedly in many parts of the neritic waters of Japan (HIRASAKA, 1922). It is often accompanied by a great mortality among fishes, molluscs and crustaceans (shrimps!) (NISHIKAWA, 1901). It is the most dreaded enemy of the pearl oyster culture (MITSUKURI, 1905, p. 284).

Records of red water and mortality are known from the following regions:

I. Bays near the entrance of the Gulf of Ise (= Owari Bay) at the Pacific side of Hondo; see fig. 7.

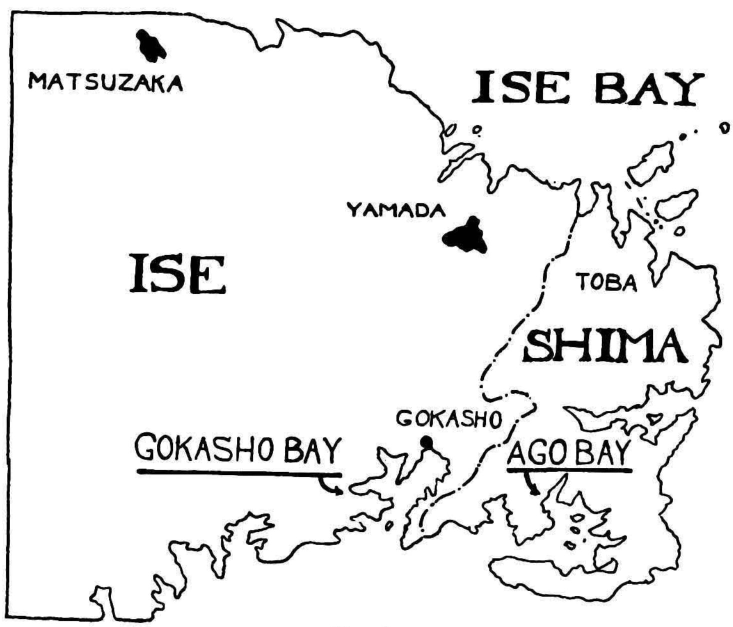

Fig. 7.

Map of the SE coast of the island of Hondo (after MIYAJIMA, 1934, fig. 1).

a. Gokasho Bay (a centre of pearl oyster industry). In the inner part of this bay (Gulf of Konsa) red water occurs in a more or less pronounced degree every winter (MIYAJIMA, 1934, p. 99); in some years it extends to the other parts of the bay too. During such heavy outbreaks it is very injurious to various animals as fishes, molluscs, etc. A very heavy outbreak occurred in 1933:

1933, November until 1934, February: A heavy outbreak of red water consisting of *Gymnodinium mikimotoi* Miyake & Kominani caused great mortality among fishes and pearl oysters. The losses of the pearl oyster industry are estimated at fifteen million yen. In connection with this disaster a method has been developed of treating the sea water with copper sulphate, which was found to rapidly destroy the red water organisms (MIYAJIMA, 1934; NIGHTINGALE, 1936).

b. Bay of Toba.

1899, latter part of August: water of a yellowish red colour caused mortality among fishes which were kept in baskets floating on the surface of the sea. "Fishermen easily caught the littoral fishes by spearing, for the fishes had become sluggish in the discolored water. Even *Haliotis* or Ear-shell seemed to suffer." (NISHIKAWA, 1901, p. 34).

c. Bay of Ago.

1900, latter part of September: red water of *Gonyaulax polygramma* Stein. Great alarm was felt for the safety of the pearl oysters; however, on the 28th of the month, a heavy storm arose and cleared the waters of the bay, so that very little damage was actually done (NISHIKAWA, 1901).

II. Tokyo Bay.

According to OKAMURA (1916, fide HIRASAKA, 1922, p. 161) the principal species of dinoflagellates causing red water in Tokyo Bay are *Cochlodinium catenatum, Polykrikos schwartzii, Pouchetia rosea* and *Gymnodinium* spec. A very heavy outbreak occurred in 1911. In 1910 and June, 1911 red water of *Cochlodinium catenatum* was very injurious to marine animals, many fishes dying as a result (OKAMURA, 1916, fide KOFOID & SWEZY, 1921, p. 45; OKAMURA in: MIYAJIMA, 1934, p. 107).

Mortality in sea caused by red water of dinoflagellates: VI. PHILLIPPINES: Bataan province (W coast of Luzon).

According to residents of the Bataan province a great mortality of fish has occurred several times along their shores (SMITH, 1908). SMITH demonstrated that this mortality is caused by red water of dinoflagellates. The observations of red water made by SMITH himself are the following: in 1908 there were at least three occurrences of red water of dinoflagellates in Manila Bay in January–March. This time they caused only a very limited mortality resulting chiefly in the death of a number of fishes in the "baclods" and in a falling off of the catches, for the schools of *Atherina* and other fishes leave the bay during red water occurrences or withdraw to places where streams enter the bay and render the water unsuitable for the dinoflagellates. With the disappearance of the fishes the fish eating birds disappear too. During one of the mentioned red water occurrences fishes and molluscs kept in a ship's aquarium fed by running water were nearly all killed after the ship had entered the bay. Every year during the prevalence of the red water the Manila markets contain much less fish than usually.

According to GENTIL (1781; fide DEAN, 1923, p. 516) a great mortality occurred at Manila in 1767; unhappily GENTIL's paper is unavailable to me.

Mortality in sea caused by red water of dinoflagellates: VII. East coast of Australia: PORT JACKSON (= harbour of Sydney).

Red water has been noticed in Port Jackson several times since 1856 (WHITELEGGE, 1891*a*, p. 145; DAKIN & COLEFAX, 1933, p. 196). In most years it is not injurious; only exceptionally it brings about a great mortality.

1866: Red water caused considerable mortality among oysters, mussels, etc. (WHITELEGGE, 1891b, p. 181).

1891, end of March: Red water consisting of a dinoflagellate described by WHITELEGGE as *Glenodinium rubrum* did considerable damage among the invertebrates of the shore fauna. According to KOFOID (1911, p. 245) this form looks suspiciously like the contents of *Gonyaulax polyhedra* Stein after ecdysis. Fully one half of the shore fauna was destroyed and the bivalves almost exterminated (WHITELEGGE, 1891b, p. 180).

According to DAKIN & COLEFAX (1933) in the years just before the publication of their paper a species of *Gymnodinium* coloured Port Jackson waters red for two or three weeks every year in July or August. Red water was conspicuous in 1930, 1931, and 1932.

Mortality in sea caused by red water of dinoflagellates: VIII. SE COAST OF INDIA: Madras coast.

According to AIYAR (1936) a great mortality of fish and invertebrates occurred on this coast in June 1935. Numerous anemones, Cavernularians, Sipunculids and countless fishes of the genera *Tetrodon* and *Diodon* in various stages of growth were washed ashore. Townet water collected at this time was almost of a soupy nature on account of the millions of the dinoflagellate *Noctiluca miliaris* present in the water. In previous years such a fish mortality had been observed too. According to MENON (1931) pink water consisting of *Noctiluca miliaris* occurs frequently on the coast of Madras in summer time.

Mortality in sea caused by red water of dinoflagellates: IX. E COAST OF U S A: Narragansett Bay.

1898, September: Red water consisting of a dinoflagellate species caused a mass mortality among fishes and crustaceans (MEAD, 1898; see further SMITH, 1900, p. CXLII; ANONYMOUS, 1899).

1900, September: Red water consisting of a dinoflagellate species caused a mass mortality of fish. Young specimens of *Cynoscion regalis* together with fish of several other species, were piled in windrows on the shore (SHERWOOD & EDWARDS, 1902).

Since 1911 there were only two occurrences of red water in widely separated parts of the bay (Prof. C. J. FISH in litt.).

The 1898 occurrence was described by MEAD (1898) as follows: During the last of August, throughout September and a part of October streaks of red or "chocolate" water were observed in a part of Narragansett Bay over a range of 15 miles, from near Quonset Point and Prudence Island north to Providence and on the flood tide upon the Seekonk river; the red colour being caused by an enormous number of a species of *Peridinium*.

On the 8th and 9th of September, as the water became extremely red and thick, myriads of shrimps and blue crabs and vast numbers of fish (eels, menhaden, tantog and flatfish) came up to the surface struggling to get out of the noxious water. Indeed the shrimps and crabs were observed actually to climb out of the water. Along the shores cartloads of dead shrimp were piled up in windrows, together with great numbers of crab and fish (especially menhaden and eels). After September 9th hardly a living crab or shrimp could be found; however, they gradually returned and three weeks after the mortality they were in the Seekonk river as numerous as before. After September 9th for a few days *Peridinium* became less abundant, and then increased again until the 23rd. At that date, however, the animals suffered no apparent injury. There was a heavy rain on the 23rd, and on the following day the water was comparatively clear.

Red water in Delaware Bay.

On the E coast of U S A red water occurs rather infrequently. It is, however, of a rather common occurrence in Delaware Bay (MARTIN & NELSON, 1927). Until now no damage to the fauna was observed. In this respect Prof. T. C. NELSON kindly informs me of the following: "Though I have observed swarming of dinoflagellates many times in Delaware Bay, swarms so heavy that the water becomes red as with blood, there has never been any mortality of fish connected therewith. The depth of the water has never exceeded 7 meters and the swarms usually fade out at night. During the last week in September, 1946, however, a very large swarm, covering approximately four square miles persisted for nearly a week close to shore in Delaware Bay. Even here, however, no fish died. The dinoflagellates in all of these swarms save one were *Amphidinium fusiforme*. The exception was a *Glenodinium*".

Mortality in sea caused by red water of dinoflagellates: X. FLORIDA COAST.

A heavy mortality among fishes and invertebrates occurs repeatedly at the Florida Keys and near the coast of SW Florida (northward to about Tampa). This mortality has been alleged by some authors to pollution of the water or a sudden change in the salinity of the sea water by sudden outbreaks of great fresh water swamps, the Everglades. This Everglades hypothesis is generally accepted in geological literature (AGASSIZ in: SHALER, 1890, p. 158; HÖFER, 1902, p. 631; ABEL, 1912, p. 37; BEEBY THOMPSON, 1925, p. 38; WEIGELT, 1927, p. 63 and 204; STUTZER, 1931, p. 309, etc.); it has, however, been stated by PIERCE (1884) and TAYLOR (1917) that this hypothesis is incorrect.

The Everglades hypothesis was based chiefly on the observation that the epidemics ensue on the presence of discoloured "poisoned" water, which could be readily distinguished from the natural blue of the Gulf. Observations of such discoloured water are given by ANONYMOUS (1881), GLAZIER (1882), GLENNAN (1887, p. 78), INGERSOLL (1882), MOORE

(1882), PORTER (1882), WEBB (1887). According to ANONYMOUS (1881), GLENNAN, MOORE and PORTER the colour of the poisonous water was reddish or brick-red; according to INGERSOLL and WEBB it was brownish. These observations make it probable, that the discoloration was caused by red water of dinoflagellates. An outbreak of red water of dinoflagellates accompanied by a great mortality in 1946/1947 confirms this supposition.

Red water and mortality occur usually in autumn. Years of very great mortality were 1878, 1880, 1916 and 1946/1947.

By some authors cases of mortality on the Florida coast are ascribed to cold (PACKARD, 1871; WILLCOX, 1887; WEIGELT, 1927, p. 84, 89; STOREY & GUDGER, 1936; STOREY, 1937; GALLOWAY, 1941). At least for some of these cases it is probable, that this supposition is incorrect.

Mortality that was very probably caused by red water of dinoflagellates occurred in the following years:

1844: INGERSOLL, 1882, p. 75.

1854: INGERSOLL, 1882, p. 75.

1878, September until about January: water of a brick-red colour occurred over a distance of at least 200 miles at the Keys and along the SW coast of Florida. In connection with the poisonous water a great mortality was observed in Florida Bay and in the vicinity of the Tortugas (JEFFERSON, 1878; JEFFERSON, PORTER, MOORE, 1878; PORTER, 1882).

1880, autumn: Great mortality in discoloured water along the SW coast of Florida, particularly about the mouth of Charlotte Harbour and off Punta Rassa. Benthonic fishes were mostly affected. Besides fishes sponges, crabs and molluscs perished in great numbers too. (ANONYMOUS, 1881; GLAZIER, 1882; INGERSOLL, 1882; MOORE, 1882).

1882, July: TAYLOR, 1917; SMITH et al., 1947, p. 1.

1883: Great mortality among fishes and other animals (oysters!) at the SW coast of Florida, particularly near Tampa Bay. "That the fish were killed by a specific poison is, proven by the sicknes and death of the birds which ate of the dead fish." The oysters were apparently very poisonous too, for it is mentioned that "the oysters came near killing several people" (WALKER, 1884).

1885, October: Fish mortality in water of a reddish colour between Charlotte Harbour and Tampa Bay (GLENNAN, 1887).

1908: TAYLOR, 1917.

1916, October—November: Great mortality between Boca Grande and Cape Romano in discoloured water; the colour being described as "black streaky", amber, olive and red. The white paint of the houses near the water was blackened. Dead fish were observed as fas as 45 miles off the coast. The dead fish observed by TAYLOR (1917) in the vicinity of San Carlos Bay ranged from jewfish of approximately 200 pounds to forms less than 2 inches long. Therefore, the size would suggest that the fishes were killed regardless of size. A long list of the species of fish affected is given by TAYLOR. The numbers of these dead fishes were representative of the relative abundance of these forms in life. Very few animals other than fishes were killed; of invertebrates only sea urchins, *Limulus* and sponges were noted.

1946, November until 1947, about August: Mortality of fish and turtles was observed in the latter part of November, 1946, 10—14 miles offshore from Naples in discoloured water. "The mortality moved northward and reached Boca Grande by January 10.

Fish continued dying in the bays behind Captiva and Sanibel Islands as late as January 29." "At Fort Myers on January 19th the beach was littered with fish in excess of 170 foot of shore line, in addition to those floating on the water in bays and sounds and to a distance of 10 miles offshore. One homeowner on Captiva Island reported burying 60,000 fish from 200 feet of bay beach." The same area had to be cleaned on more occasions. Besides fish and turtles, oysters, clams, crabs, shrimps, barnacles, and coquina were also killed (GUNTHER, SMITH, WILLIAMS, 1947). The mortality continued in a more or less continuous series of outbreaks until August 1947 occurring at various places between Key West and Sarasota, and between the shore and a line situated twenty miles or more offshore (SMITH et al., 1947; ANONYMOUS, 1947). The total quantity of the dead fish was in the order of nearly half a billion.

The discoloured water was of an amber yellow colour; it gradually changed and became red or dirty green. The discoloration was due chiefly to a species of *Gymnodinium* (see DAVIS, 1948).

During these occurrences of red water and mass mortality the occurrence of a "gas" has been reported causing respiratory irritations of people living near shore (TAYLOR, 1917, p. 7; GUNTHER, SMITH, WILLIAMS, 1947). This phenomenon has been studied by WOODCOCK (1947*a*, 1947*b*). It turned out that the irritations may be associated with the presence of small drops of "red water" in the air.

Besides the cases of fish mortality occurring in red water consisting with certainty of dinoflagellates other cases are known in which the nature of the discoloration has not been examined.

Mortality in sea caused by red water (probably consisting of dinoflagellates): XI. UNION OF SOUTH AFRICA: Cape Province.

Red water of dinoflagellates occurs rather frequently in South African seas (GILCHRIST, 1914). Several records are known from the Cape Peninsula. In some bays it may be seen several times in the southern summer, being often of an almost blood red colour (GILCHRIST, 1914, p. 17). According to this author the red colour is due to a species of *Noctiluca*. HART (1934*a*) mentions that *Noctiluca scintillans* may be indeed a cause of red water in the sea off South Africa in summer, the red water sometimes seen near the Cape of Good Hope is, however, probably caused by a dinoflagellate of the genus *Gymnodinium* (HART, 1934*b*, p. 170).

Fish mortality has been recorded frequently from the vicinity of Cape Town and also from other parts of the southern coast of the Cape Province. According to GILCHRIST (1914, p. 32) such mortalities do not seem to occur in Natal; they are confined to the coast extending from East London on the east coast round the S coast to somewhat north of Saldanha Bay on the W coast. While at most places the occurrence is more or less intermittent, at Knysna it is an annual phenomenon. Dr. J. PRINGLE, the director of the Port Elisabeth Museum, informs me, that mass mortality of fish occurs every few years along the Schoenmakers Kop coast. An extensive mortality occurred on 19th January 1946, extending along the coast from Schoenmakers Kop to Jeffreys Bay.

The supposed causes of the mortalities on the South African coast are according to GILCHRIST for the most part rather obscure. Some cases of mass mortality are attributed by this author to noxiousness of red water of dinoflagellates. As red water occurs frequently on this coast the possibility is not excluded that red water is also responsible for some of the other mortalities recorded from this coast, e.g., those at Knysna and at Schoenmakers Kop.

The cases attributed by GILCHRIST (1914) to noxiousness of red water are the following (the cause of the red colour or of the phosphorescence was not examined):

Stumpnose Bay (an open Bay to the north of Saldanha Bay):

About 1869: A great mass of Geelbek fisk were found swimming, head above water, apparently in a stupified condition in dark red water.

Saldanha Bay:

About 1907: "The bay was filled with red water. The fish in the bay were seen floating belly upwards in a disabled condition. Some of them were cast on shore at the end of the bay in such numbers, that they were taken away in cartloads. Even the shell-fish, such as mussels (*Donax serra* probably), Klip-Koes (*Haliotis*) were killed off in large numbers."

Table Bay:

About 1888: "The water of Table Bay, after darkness had set in, appeared like a sea of phosphorus. Many persons were taken ill, and I believe some died after eating fish, especially shell fish. I myself saw several baboons lying dead on the beach near Simon's Town with clam shells in their paws."

It seems probable that the death of many persons and baboons by eating shell fish that were captured in very phosphorescent water is a case of mussel poisoning by a dinoflagellate poison (see the following chapter).

Mortality in sea caused by red water (probably consisting of dinoflagellates): XII. NW COAST OF INDIA: Kathiawar.

According to CARTER (1858, p. 262) red water is extremely common at Porbandar (Kathiawar). On the 27th October 1849 the colour of the sea water was changed to a deep red, emitting a most foul smell: the fish speedily were all destroyed, and were washed upon the beach in large quantities. CARTER supposes that the red colour was caused by "some animalcule, most probably a *Peridinium*."

Mortality in sea caused by red water consisting probably of dinoflagellates: SOUTHERN PART OF RED SEA AND GULF OF ADEN.

In 1902 a very great mortality was observed by ILG (1902, fide HÖFER, 1902, p. 634) in brownred water in the southern part of the Red Sea and the Gulf of Aden. Among the fishes floating on the surface of the sea "die Meereshyäne und der Hai" were particularly frequent. The dead fish were carried by an eastwind to the African coast. The odour of putrefaction was so intense that in regions under European management the order was given to bury the fish. When ILG disembarked at Jibuti hundreds of hundredweights of sharks were drawn on land.

According to general opinion (EHRENBERG, 1830; MONTAGNE, 1844; DARESTE, 1855; CARTER, 1858; STEUER, 1911; OLTMANNS, 1923; SVERDRUP, JOHNSON, FLEMING, 1946, p. 289; etc.) the Red Sea owes its name to red water of blue algae. Exact records of this phenomenon are the following: EHRENBERG (1830) observed bloodred water in the Bay of Tor on 10, 25 and 30 December 1823 and on 5 January 1824 caused by *Trichodesmium erythraeum* Ehr.; it was observed only in the bay and not in the open sea outside of it. On 15—VII—1843 the whole sea from Cosseir to Tor had according to DUPONT (fide MONTAGNE, 1844, p. 336) a red colour, being caused by the same organism. Another observation was made by MÖBIUS (1880) between 23° and 25° N.

Except by blue algae a red discoloration of the Red Sea may, however, be caused by other organisms too, e.g., by dinoflagellates. The observations of JOAO DE CASTRO in 15° 35′ N on 24—II—1541 (fide DARESTE, 1855, p. 207) and of SALT in 15° N on 7—II—1810 (fide DARESTE, 1855, p. 207) that the Red Sea was red by day and luminescent by night very probably refer to dinoflagellates. CARPENTER & WILSON BARKER (1915) mention concerning red water of dinoflagellates: "The writer has seen the Red Sea by day looking as if covered by floating reddish sand. On collection it was found to be made up of countless numbers of *Noctiluca*, a small jelly about the size of a pin's head. Each jelly had an orange-red central spot which after dark emitted phosphorescent light. Thousands of tons of *Noctiluca* are sometimes washed on shore in the Red Sea, and the beach appears covered with piles of blood. When fish find themselves in one of these brilliant swarms they seem to go quite mad."

The redbrown colour observed by ILG during the 1902 mortality in the southern part of the Red Sea and the Gulf of Aden, therefore, may have been caused either by blue algae or by dinoflagellates.

On my inquiry if red water and/or mortality had been observed in recent years in this region the Chief Secretary at Aden and Mr. C. H. INGE (further also Mr. J. GAEPEL) gave me the following information:

1. Red Sea: Kamaran Island near the coast of Jemen.

The following observation has been made by Mr. D. THOMPSON (Kamaran): On 23rd August 1947 the sea over the area including Kamaran harbour and Kamaran Bay but excluding a clear belt of one mile along the Jemen coast line became copper or bronze colour. Phosphorescence is, of course, a feature of the Red Sea, but this year it has been very brilliant, creating a marvellous spectacle at night with fish large and small darting about like streaks of silver.

The sea continued to darken with a deep red colour and on 1st September hundreds of fish of medium and small sizes were hurling themselves on the beaches, all in a state of what might be termed helpless intoxication.

Besides fish various kinds of invertebrates died too; these were chiefly cray-fish, small crabs and prawns. There were also reports of sea snakes having beached and died.

The sea began to give off an offensive smell acrid and sulphuric. It has been ascertained from masters of pilgrim ships that the conditions described extended beyond Kamaran Bay to a distance of five miles south of Risha Island. The red discoloration of the sea is an annual event, but the phenomenon witnessed in 1947 seems to occur on rare occasions only. The nature of the red discoloration is not known with certainty.

2. Vicinity of Aden.

A red discoloration of the water occurs often in summer in this region. August 1944 a great mortality among small fish occurred along the 40 miles of coast immediately north east of Aden. It has not been established if the mortality occurred in red water.

A yellow discoloration of the sea has been observed from the air on several occasions between Bir Ali and Mukalla, about 250 and 300 miles east of Aden.

It remains to be investigated whether the following cases of mortality indeed are caused by noxiousness of phytoplankton. They are recorded only to stimulate research in the localities mentioned.

Mortality in sea in yellow water: COAST OF YUCATAN (Mexico).

M. (1908) describes the following occurrence from the vicinity of Progreso in the fall of 1907: about 8 miles off the coast the water had a yellow colour and was covered with an immense quantity of dead fishes. Millions of dead fish drifted ashore on the Progreso beach. The nature of the yellow colour is unknown. BEEBY THOMPSON (1925, p. 235) mentions also a great mortality from the same region, the sea being covered with an oily scum; at that time so many dead fish were washed ashore that the Mexican authorities had to engage troops to destroy the decaying masses. Such an oily scum often derives from dead plankton being present in a great quantity; cf. the occurrence of scum after aguaje p. 52. Therefore, it seems probable, that the fishes died by noxiousness of phytoplankton.

Mortality in sea in discoloured water: COAST OF CHILE.

Mass mortality of fishes and squids (*Dosidicus gigas* (Orb.)) occurs repeatedly along the coast of Chile; the mortality of squids being particularly conspicuous. D'ORBIGNY (1835—43) remarks in this respect: "Nous avons vu la mer couverte de débris d'Ommastrèphes, surtout au mois de février et de mars, en approchant des côtes du Chili par 33 degrés de latitude sud; et à la même époque, nous en avons vu jetés en grand nombre, encore vivans, à la côte de Valparaiso, sur toute celle du Chili, de la Bolivia et du Pérou, à Cobija, au 23^{e} degré de latitude sud, puis au port d'Arica."

The mortality seems to occur most often and in the most heavy degree in the Bay of Talcahuano and in the nearby Bay of Arauco. Here it occurs nearly annually; in some years the mortality is extraordinarily great. Still more southerly mass mortality occurs too, for RAHM (1937, p. 1245) mentions that it occurs at the mouth of the Valdivia river and even as far south as Chiloé. Among the inhabitants of Chiloé the mortality is well-known, they use the dead squids for manure.

The mortality occurs nearly in the same season as at the coast of Peru, that is from the end of February to mid April. Great mortalities were observed in the Bay of Talcahuano at the following dates:

1895, 7—11 February: CIENFUGOS, 1895; SCHNEIDER, 1930, p. 120.
1916: SCHNEIDER, 1930, p. 130.
1930, April: SCHNEIDER, 1930, p. 120. Photographs of this mortality are given by WILHELM (1930; 1932) and by GUNTHER (1936a).
1932: FALKE, 1939, p. 658.

Various hypotheses have been put forward with regard to the cause of this mortality. It was ascribed by CIENFUGOS (1895) to volcanic gazes escaping from the bottom of the bay. According to WILHELM (1930; 1932) the harbour is a very unfavourable locality for squids; many of them being killed as a result of battering against rock or quay side. Death by H_2S originating from the sediment that is very rich in organic material is proposed by WILHELM as second possibility. SCHNEIDER (1930) gives the following two possibilities: physiological death after spawning and death by impureness of the harbour water. Hypotheses connecting the mortalities with peculiarities of the harbour must be incorrect, because the mortality is not confined to the harbour at all.

According to FALKE (1939) the mortality is caused by H_2S deriving from the decay of enormous masses of plankton. FALKE points to the fact that contrary to the situation in the southern winter the production of the phytoplankton in the Bay of Talcohuano is enormous in the southern summer. By these great masses of plankton the colour of the water at the end of December becomes yellow or yellowgreen; some weeks later (at the time of the mortality) the colour of the water becomes milky. The milky discoloration was already observed by CIENFUGOS (1895): The colour of the water changed completely; the whole surface of the water had a milky appearance over a distance of many miles. The milky colour of the water is according to CIENFUGOS caused by sulphur originating from volcanic gazes. SCHNEIDER (1930) emphasizes that the milky appearance is due to a very little crustacean. According to FALKE (1939) it is caused by H_2S.

There is a pronounced similarity between this periodically occurring mortality and those along the coasts of Peru (cf. the milky colour observed by HUTCHINSON at the end of aguaje, see p. 52), of SW Africa, etc. Therefore, it is possible, that it has a similar or a related cause, viz., noxiousness of dense populations of certain elements of the phytoplankton.

It will be set forth in chapter IX that red water and mass mortality occur especially in regions of upwelling water. Therefore, it seems worth while to describe the following mortalities occurring in regions of upwelling, although it is until now unknown whether they occur in red water indeed.

Mortality in sea: Region of upwelling water at the COAST OF NW AFRICA.

1. Senegal.

On my inquiry if red water and/or mortality occur on this coast Dr. J. CADENAT (the director of the Zoological Station at Gorée, near Dakar) informed me that mass mortality of fishes and invertebrates occurs indeed on the coast of Senegal.

a. Region of Dakar.

Nearly every year, during the period extending from February to April, mass mortality of fishes, especially of Clupeidae and Engraulidae, occurs in the southern part of the peninsula. In that period of the year 1939 the mortality was so enormous that the Public Health Service had to ask for help from the military authorities to clear away the dead *Sardinella eba* that were cast on the beaches in the region of Hann. On 17 February 1944 the banks of *Ethmalosa fimbriata* were so dense in the immediate vicinity of the coast that nearly 150 tons of these fishes penetrated in the dry docks of the harbour of Dakar in the moment of the entering of a ship and that by one stroke with the seine in the bay of Hann more than 17 tons were captured. In the next day enormous masses of these fishes died on the coast.

On the 25th of March 1946, at Gorée anchovies (*Engraulis hepsetus*) penetrated into the small harbour of the island in enormous masses and died. Besides the anchovies a great number of other fishes died too: Blennidae, Gobiidae, Labridae (*Thalassoma, Coris*), Gobiesocidae (*Lepadogaster*), Scorpaenidae (*Scorpaena, Scorpaenoides*), Muraenidae, Pomacentridae, etc. Moreover, a very great number of invertebrates perished: worms, echinoderms, molluscs, crustaceans, etc. (CADENAT, in litt. and 1946).

b. Region of Joal.

At the end of the dry period and the beginning of the winter (June—July), mass mortality of fishes as well as invertebrates occurs rather periodically; for instance from 24—28 July 1943 and from 30 June—4 July 1944. Among the perished fish Apodes were most abundant. The following dead invertebrates were observed: Coelenterates (actinians), molluscs (resistant species as *Ostrea parasitica* and *Senilia senilis* included), crustaceans (*Palinurus regius,* Calianassidae, Squillidae, etc.).

The cause of these mortalities is not yet known. Dr. CADENAT supposes with regard to the Dakar mortality that the migratory fishes (when they are exhausted after reproduction) are pushed by winds to the coast, where they die; these dead fishes would cause the death of the other fishes and of the invertebrates. With regard to the Joal mortality Dr. CADENAT supposes that the fishes and the invertebrates are poisoned by H_2S, developing by the decomposition of weeds and Cymodoceans, and ascending from the black muddyish sand and the black mud occurring in this part of the sea.

These hypotheses should not be rejected. However, these periodically occurring mortalities remind of similar occurrences in other regions of upwelling water and, therefore, the possibility is not excluded that they are caused by noxiousness of red water too.

2. Surroundings of Cape Blanco. On my inquiry if mortality occurs also near Cape Blanco Dr. TH. MONOD drew my attention to a passage in an old book by VALENTIN FERNANDES (vide CENIVAL & MONOD, 1938, p. 67) that a great mass of dead fishes had been observed on the beaches of the islands in the Arguin region (Atlantic Saharian coast about 20° 30′ N) and on the sea bottom around these islands; a horrible odour was given off by these dead animals.

A brownred discoloration of the water occurs frequently at the Saharian coast of NW Africa; PUFF (1890, p. 27) writes concerning the region of Cape Nun: "In einiger Entfernung sowohl nord- als südwärts des Kap Nun, ebenso auch weiter in der See hat das Wasser eine rothe Farbe nebst einem dicken schmutzigen Aussehen, so dass die Spur des Schiffes noch einiger Zeit sichtbar ist". The discoloration is ascribed to Saharian sand falling into the sea. Indeed dust fall occurs frequently on this coast (see SCHOTT, 1942, fig. 79) and, therefore, part of the discolorations may be caused by dust; it is, however, very probable that another part is caused by dense populations of phytoplankton.

Mortality in sea: Region of upwelling water at the SOUTHERN COAST OF CEYLON.

On my inquiry whether red water and/or mortality ever occur on this coast Dr. P. E. P. DERANIYAGALA (the director of National Museums, Ceylon) informed me that there was a great fish mortality of the species *Diodon hystrix* in November 1933. They came up dead and dying from Colombo to Hikkaduva, a distance of about 30 miles along the coast. "During other years a few specimens of *Diodon* are washed ashore but I have never seen them in such quantity." The mortality lasted for three weeks. The cause of the mortality is unknown.

Mortality in sea: Region of upwelling water at the COAST OF VENEZUELA.

Fish mortality occurs repeatedly near Carupano; CLARK (1903, p. 285) mentions in this respect: "at certain times fish run ashore here by the cartload". The cause of this episodically occurring mortality is unknown.

GENERAL CONCLUSIONS on the noxiousness of blue algae, flagellates and dinoflagellates:

In fresh water most cases of fish mortality occur in connection with waterbloom of blue algae; on the rare occasions of a mass development of dinoflagellates in fresh water they seem to be also noxious to fish.

In brackish water several cases are known of mortality in connection with mass development of blue algae, flagellates as well as dinoflagellates.

In sea until now only some rather insignificant records of mortality are known to occur in water with waterbloom of blue algae. From one region (Malabar and Kanara coasts) it is known that a great mass mortality occurs periodically in water coloured reddish amber by flagellates, while from several parts of the world a great mass mortality is reported to occur in red water of dinoflagellates.

However, red water of dinoflagellates is surely not always injurious. In Delaware Bay for instance red water occurs frequently, but mortality has not yet been observed. In the other regions mentioned above, red water is at one time injurious, whereas at another time no injury is observed at all. Whether mortality occurs or not depends on the following: A first requirement is that the red water outbreak is very heavy, that is the water must become extremely thick and red, the number of cells per liter being very high. Further it is important that red water occurs over a vast area, so that escape is prevented. Moreover, it is possible, although not certain, that only some species or genera of dinoflagellates may be injurious, whereas other dinoflagellates may not be injurious even if they occur in very large numbers. Until now mortality in sea has been observed in red water consisting of species of the genera: *Gonyaulax* (California, Port Jackson (SE Australia), Japan), *Gymnodinium* (Florida, Washington State, Japan), *Cochlodinium* (Japan) and *Noctiluca* (SW Africa, Madras). In brackish water mortality occurred at a yellowish waterbloom of *Heterocapsa* and *Glenodinium*.

Along the coast of S California mortality has been observed only during occurrences of red water of *Gonyaulax polyhedra* Stein. In 1938 and 1945, however, mortality did not occur, although this species was very abundant. High abundance of a notorious species is, therefore, not always sufficient to cause mortality (ALLEN, 1941, p. 632).

Along the coasts of SW Africa, Peru, Japan, Malabar coast and probably also in some other regions (NW Africa?) conspicuous occurrences of red water may be observed nearly every year. In these regions some mortality seems to occur nearly annually too. In several years the mortality is limited and, therefore, will not be recorded unless special attention is paid to the phenomenon; see for instance the annual occurrence of some mortality at the Malabar coast observed by HORNELL and the annual occurrence of some mortality near Walvis Bay observed by CLASSEN. The rarity of the phenomenon may, therefore, be only apparent. At the coast of S California, however, the number of observations is so high, that it is beyond doubt that conspicuous occurrences of red water are rare, mortality being still more rare. Between 1894 and 1945 mortality was observed only four times: 1894, 1901, 1907 and 1917. Mortality, therefore, occurs in one region much more frequently than in another.

In all regions in certain years the mortality is extraordinarily great; obviously in such years the circumstances are very favourable to great outbreaks of red water. It is uncertain whether very pronounced outbreaks of red water occur particularly in years of great meteorological disturbances (see Peru and Walvis Bay).

In years of limited mortality it occurs probably chiefly close inshore, particularly in the rather sheltered water of embayments that favour intense concentrations of red water (see Malabar coast). In years of great mortality, however, it seems to occur several miles offshore too; cf. Malabar, Florida and California coasts.

Red water and mortality occur in several regions at a certain time of year; Walvis Bay region: southern summer, particularly in December/January, great mortalities mostly at Christmas time; Peru: chiefly between December and April; ?Talcahuano: February until April; Malabar coast: end of August until beginning of November; Florida coast: most often in autumn. In those regions a favourable combination of factors needed for great outbreaks of red water (see chapter IX) apparently occurs at a certain time of year only. Along the coast of Japan red water occurs in summer as well as in winter. Sometimes the phenomenon may last during several months; at least at the coast of Japan (November 1933 until February 1934) and of Florida (November 1946 until August 1947).

The animals affected by red water are vertebrates as well as invertebrates. The dead vertebrates are chiefly fishes; however, if aquatic vertebrates other than fishes are present, they may be also affected: sea turtles (Florida), sea snakes? (Kamaran, Red Sea). Further terrestrial vertebrates may be affected too by eating the poisonous aquatic animals: birds and seals poisoned by eating fish? (SW Africa, and Florida, 1883); baboons poisoned by eating clams? (Table Bay, 1888); man poisoned by eating molluscs (Florida, 1883; see further following chapter).

Of fishes benthonic living forms are in most regions affected in the first place, whereas pelagic fishes are affected only if the mortality is very great. At the Malabar coast in years of limited mortality the fish affected almost exclusively belong to benthonic living species (soles!); only in the years of extraordinarily high mortality the schools of sardines are affected too. In the Walvis Bay region on the first day of a mortality benthonic living species (soles!) almost exclusively drift ashore, on the following days various pelagic species.

The reason for the annual shoreward migration of the sardines at the Malabar and South Kanara coasts is to feed upon the immense quantities of dinoflagellates and flagellates developing in autumn in coastal waters (HORNELL & RAMASWAMI NAYUDU, 1924). The same reason may be the inducement for the shoreward migration of the sardine schools near Walvis Bay and NW Africa sometimes resulting in a great catastrophe.

Various groups of invertebrates are affected by red water. Especially crustaceans (crabs, shrimps, etc.) suffer greatly (Malabar coast, California, Peru, Narragansett Bay, Florida, Kamaran (Red Sea)). From both the Malabar coast as well as from S California it has been mentioned, that great numbers of *Hippa* species were thrown on the beach. Molluscs may be greatly affected too; the latter applies particularly to cephalopods (California, Peru, and Chile (if the latter mortality is caused by red water indeed)). Other molluscs may perish in great numbers too (Malabar coast; Peru; Japan (pearl oysters!); Florida; Saldanha Bay (S Africa)).

During severe outbreaks of red water a great percentage of the benthonic invertebrates is massacred (see Port Jackson 1891, etc.). In such regions where great outbreaks of red water occur very often (Walvis Bay region) benthonic invertebrates will be completely exterminated over great areas. Therefore, the dead animals found on the beach of Walvis Bay are nearly exclusively fishes. In regions where mass mortality occurs on rare occasions only, it will, however, have only a temporary influence on the shore fauna.

According to Dr. SCHWEIGGER, to whom I am indebted for the following valuable information, great mortalities apparently are more rare at the coast of Peru than near Walvis Bay (in a book by SCHWEIGGER that will appear before long, the Peru occurrences will be treated of in detail). The blood red spots, occurring frequently along the coast of Peru wherever warm water invades the cool coastal water, merely are avoided by fish. If fish are enclosed in areas of red water approaching the coast, they only get stunned, and in this state they are thrown on the beach. Similar observations have been made in other regions (see the observation on 13—II—1928 at Walvis Bay, mentioned on p. 17 of the present paper, and those in the Bay of Toba (p. 54), Stumpnose Bay (p. 59), and near Kamaran Island (p. 60)). Of the animals thrown up on the beach of San Pedro in 1901 (p. 48) a part was dead, whereas others lived for several days. According to HORNELL (1917, p. 53) "the first effect of the poison is to make the fish sluggish"; if the poisonous effect increases, fish die in great numbers near the coast as well as in the open sea. It seems probable that this occurs also in exceptional years at the coast of Peru.

CHAPTER VII.

Hypotheses on the noxious effect of "waterbloom".

From the records given in the former chapter it will be obvious that it is not a mere hypothesis, but a well established fact, that red water of dinoflagellates may cause mass mortality. Opinions greatly differ, however, as to the question how the mortality is brought about. The same applies to the noxious effect of waterbloom of blue algae and of flagellates. Research work of the last decennia has shown that these organisms sometimes, in the living state, produce a powerful toxin (perhaps at a certain stage of their life). Therefore, the hypothesis seems reasonable and in some cases has even been proved, that the noxious effect is a poisoning by such a toxin; the possibility is, however, not excluded, that sometimes other factors (exhaustion of oxygen at night in freshwater lakes, etc.) may worsen the situation.

1. BLUE ALGAE.

With regard to the assumption that waterbloom of blue algae may bring on fish mortality in fresh water STRODTMANN (1898) claimed that waterbloom is only indirectly noxious, the mortality being caused by lack of oxygen or by poisons following the decay either of the plankton or of other organic substances. This conception has been adopted by many authors (LAMPERT, 1899, p. 512; 1925, p. 589; STEUER, 1910, p. 676; idem 1911, p. 357; REDEKE, 1916; VAN GOOR, 1920; etc.). It is, however, important that waterbloom may be very noxious not only to fishes, but also to air breathing animals as cattle and fowl (cf. p. 40), for which lack of oxygen in the water is of no importance. In water samples collected during occurrences of blue algae waterbloom, accompanied by cattle and fowl mortality, FITCH et al. (1934) have demonstrated a very powerful toxin; the latter being produced by the living blue algae plankton. This poison was an organic compound of small molecular weight, disappearing upon putrefaction of the algae.

2. FLAGELLATES.

CONRAD & LELOUP (1938) assume that the central, short and stiff flagellum of the flagellate *Prymnesium parvum* Carter 1938 may penetrate into the gills of the fish causing their death. OTTERSTRØM & STEEMANN NIELSEN (1940, p. 23) have pointed out, that the stiff flagellum has nothing to do with the noxiousness of the flagellates. They agree with the opinion of LIEBERT & DEERNS (1920) that the noxious effect is a poisoning; the toxin being produced by the flagellates during their life. According to

LIEBERT & DEERNS (l.c.) the effect of the poisoning is a haemolysis. OTTERSTRØM & STEEMANN NIELSEN could not confirm this supposition. In the experiments of the latter authors the respiration of the fish appeared to be highly influenced; it seemed questionable, however, whether a suffocation as such was the cause of death, universal paralysation of the nerves being more probable.

As to the noxious effect of the olive brown water of flagellate B in the sea at the Malabar coast, HORNELL (1917, p. 63) makes three suppositions: 1. exhaustion of oxygen in the sea water; 2. poisoning by excretion products of living flagellates or by the products of decomposition liberated by the death of the short living generations; 3. asphyxiation by blanketing of the fish with a mass of flagellates that have passed into the jelly forming resting stage (cf. p. 44).

With regard to the paralysing effect of the flagellate *Prymnesium parvum* Carter it is probable that the effect of flagellate B is similar. As the poisonous water occurs annually at the Malabar coast, the truth of this supposition could easily be tested.

3. DINOFLAGELLATES.

As to the noxious effect of red water of dinoflagellates the supposition was made by several authors (NISHIKAWA, 1901; KOFOID, 1911; LINDEMANN, 1924; MARCHAND, 1928) that the death of fishes and invertebrates is caused by the accumulation of toxic substances in the sea water following the decay of large quantities of (nitrogen bearing) plankton. A second hypothesis is that the myriads of dinoflagellates cause asphyxiation of the fishes and invertebrates by clogging the gills. In view of recent researches on paralytic shellfish poisoning, by which it is shown that a powerful toxin may be produced by living dinoflagellate plankton, this assumption probably has to be revised.

Paralytic poisoning of man by eating mussels is rather rare in Europe. According to KOCH (1938) records of mussel poisoning are known from the following places: Wilhelmshafen (Germany) in 1885 and 1887; near Dublin (Ireland) some years after 1887; Christiania (= Oslo, Norway) in 1901; Calais (France) in 1907. KOCH (1938; 1939) himself described some fatal cases of mussel poisoning from Belgium (mussels deriving from the canal Bruges—Zeebrugge) in June 1938.

At the Pacific coast of North America shellfish poisoning is a rather commonly occurring phenomenon (upwelling water; see chapter IX). An extensive investigation of this phenomenon was started in California in 1927. Numerous communications from physicians and other persons brought out the fact that at certain parts of the coast annual occurrences of intoxications are the rule rather than the exception. It concerns group intoxications of man and domestic animals. Mass intoxications of Indians and single poisonings of white settlers, which occurred about half a century ago are also recorded.

Mussel poisoning occurs only in the summer months, between May and October. As a result of the investigation of the toxicity in Central California it turned out that in most years the maximal toxicity is reached about the middle of July in localities south of San Francisco and somewhat later in those north of this place. Early in spring the toxicity curve rises to a second maximum, which usually persists until May or June. Then a peculiar drop of the curve occurs, before it rises sharply to the summer maximum. Only at the summer maximum the curve rises above the danger line for man.

In European cases the poisonous mussels derived from ports, estuaries or canals. At the Pacific coast the poisonous mussels occur at the open shore of the ocean.

Many theories have been proposed for the explanation of the occurrence of poison in shellfish. The more likely ones are enumerated in MEYER, SOMMER & SCHOENHOLZ (1928). Most of these hypotheses have been refuted by the Californian investigations (MEYER, 1931; SOMMER & MEYER, 1937), for "it became more and more apparent that the agent responsible for the toxicity was contained in the ocean water and approached the shellfish beds more or less periodically from offshore. Since the hypothesis that the toxic agent was an organism pathogenic for mussels, or the assumption that the toxicity was due to an actual disease did not receive any support, the search for the causative factor narrowed down to a dissolved or particulate substance in the water which the mussels were taking up. It was obvious that the food of the shell-fish, i.e., the diatoms and the dinoflagellates were one possibility." (SOMMER et al., 1937, p. 537). It turned out that there was a close relation between the number of certain dinoflagellates and the poisonousness of the mussels, the annual maxima of certain species of the dinoflagellate genus *Gonyaulax* appearing to occur preceding and during each poison period. Diatoms may be excluded from consideration as a factor for the production of the poison, as there was no accompanying increase in the quantity of poison extracted from mussels collected at the times of maxima of diatoms.

In the San Francisco region the toxicity of the mussels is chiefly caused by *Gonyaulax catenella* Whedon & Kofoid, although other species of *Gonyaulax* may perhaps be responsible too. Accompanying all increases of the poison, both major and minor, the colour of the cell content of these *Gonyaulax* species which is normally yellowgreen or golden, assumed a reddish brown or orange brown cast in most of the individuals (WHEDON & SOMMER, in: SOMMER et al., 1937, p. 546). "The rapid increase in the number of *Gonyaulax catenella* which preceded each period of poison in the mussels and was accompanied by color variations is possibly to be attributed to a specific stage in the life cycle of this organism." (SOMMER et al., 1937, p. 548).

(Independently of these researches KOCH (1938; 1939) arrived at the conclusion that the toxicity of the mussels in the canal Bruges—Zeebrugge in 1938 was caused by a dinoflagellate occurring in great quantity. This dinoflagellate was described by WOLOSZYNSKA & CONRAD (1939) as *Pyrodinium phoneus.*)

In 1933 the poison was isolated directly from dinoflagellate plankton (SOMMER et al., 1937, p. 553). The poison isolated from plankton was found to be identical in all respects with an extract of poisonous mussels, i.e., solubility (solubile in water and alcohol, insolubile in ether and chloroform), stability (stabile towards acids, instabile towards alkali) and symptoms in experimental animals, viz., in mice (central paralysis, strong spasms, heart block). Further it has been made probable by SOMMER and co-workers that not only paralytic shellfish poison, but also other poisons occurred in the phytoplankton. (For the effect of paralytic shellfish poison on nerve cells, see COVELL & WHEDON, 1937).

Shellfish collected during an occurrence of red water at La Jolla in May 1933 caused chiefly by large numbers of *Ceratium* and *Prorocentrum,* contained a poison that was distinct from normal paralytic shellfish poison in so far as its action on experimental animals is somewhat different: it acts after a longer incubation time.

Besides mussels of the species *Mytilus californianus* other bivalves and crabs (SOMMER, 1932) may be highly toxic too. A rather high mortality occurring often among the crabs at the coast of Central California is probably due to the noxious effect of shellfish poison. Shellfish themselves appear to be resistant to comparatively large quantities of the poison; the same applies to other cold blooded invertebrates and vertebrates (PRINZMETAL, SOMMER & LEAKE, 1932). "Proportionally larger doses of the poison had to be injected into frogs than into mice, dogs or cats to produce symptoms of mussel poisoning. A salamander, *Batrachia,* commonly found in gardens in the vicinity of San Francisco, has been found to be at least forty five times more resistant to the poison than the average-sized laboratory mouse used in determining the toxicity of the mussels." (SOMMER et al., 1937, p. 548).

Although the resistance of cold blooded animals to paralytic shellfish poison is much higher than that of warmblooded animals, it seems highly probable that this or a related poison produced in the living dinoflagellate plankton is the cause of the mass mortality of fishes and invertebrates occurring in red water of dinoflagellates in various parts of the world. This conception is advocated already by SOMMER et al. (1937, p. 547) with regard to the mortality of marine animals during the San Diego occurrence of red water: "Quantities of shellfish-poison, much larger than have been measured in the San Francisco region, quite possibly existed in the living plankton at that time, but since tests for toxin were not made this cannot be checked. Perhaps if the numbers of *Gonyaulax catenella* and related species associated with it during the present investigation had been greater, the quantities of poison extracted from the digestive glands of the mussels might have been many times larger than the tests have indicated, and the poison, possibly of sufficient potency to have caused either metabolic disturbances in the mussels or their death."

Since mortality due to red water occurs only sporadically along the Californian coast, it may be several years before this hypothesis can be tested. In Walvis Bay, however, some mortality seems to occur annually. This is, therefore, the obvious place to test the hypothesis, that the mass mortalities of fishes are brought about by a poison identical with or related to paralytic shellfish poison, and, therefore, being produced by the living dinoflagellates during occurrences of red water.

CHAPTER VIII.

Upwelling water and the organic production in the sea.

Conditions governing the production in the sea have been reviewed frequently in oceanographical literature (for recent outlines see SVERDRUP, JOHNSON, FLEMING, 1946; CUPP, 1943; GILSON, 1937; WISEMAN & BENNETT, 1940; HART, 1942, etc.). It is, however, necessary for an understanding of the present paper to give a short survey.

For the production of phytoplankton various physical and chemical factors are required: light, water, carbon dioxide, oxygen, phosphates, nitrates or ammonium, silicates, and various secondary elements as iron, manganese, etc. If one of these factors is present in a very small amount, it acts as a limiting factor for the plankton growth. The chief limiting factors regulating the production of the phytoplankton are light and nutrients (chiefly phosphates and nitrates are concerned). Light is a limiting factor in temperate and high latitudes in winter. Further it controls the thickness of the water layer in which photosynthesis takes place. Temperature probably does never limit the production of the plankton as a whole, but it undoubtedly does affect its composition. Dinoflagellates for instance in temperate regions always have their maximum in the warm summer months. Phosphates and nitrates are generally present in a very small quantity; therefore, they often act as limiting factors. The production of the phytoplankton is, therefore, closely dependant on the supply of these nutrients in the well lighted upper layers of the sea (theory of BRANDT, 1899, 1902, 1920, 1929).

By the growth of the phytoplankton the nutrients are removed from the surface layers and sink downwards in insoluble form with its dead and dying cells, or in the bodies or excrements of animals eating it. In deeper water layers either en route or on the bottom the nutrient elements are mineralized and again become soluble. The quantity of nutrients in the surface layer can be renewed in two ways; either from the shore (rivers, rivulets, etc.) or from deeper water layers.

The supply of nutrients by river water is in many cases insignificant, as the nutrients are consumed by organisms living in the rivers themselves; this has been shown by ATKINS (1923; 1926) for the Plymouth Sound region. Some rivers, however, have an important effect indeed. RILEY (1937) has shown that the Mississippi river carries large quantities of nutrients into the Gulf of Mexico, the quantity of phosphates near the mouth of this river being considerably higher than in the surrounding region. HARDENBERG (1931, and personal communication) has found that the quantity of nutrients and the production in the Java Sea are generally low with exception of the regions off the mouth of the great rivers of East Sumatra and Borneo.

From deeper layers in the sea the nutrients gradually return to the upper layers by diffusion. However, the process of diffusion takes place much too slowly in motionless water to compensate the consumption by the phytoplankton. The nutrients may, however, be carried quickly upwards in another way; that is by vertical water movements. This occurs in the following way:

1. CONVECTION.

Convection currents appear if the density of the surface water is increased beyond that of the underlying strata. The density increases by cooling, by evaporation and by the formation of ice (because the salinity of the water surrounding the ice crystals increases). Intense cooling of the surface water in a certain time of the year and the formation of ice occur in temperate and cold regions only. In the tropics and the subtropics the temperature of the surface water is high all the year round, and, therefore, the density always remains low. In the open ocean it even remains low in such regions where a great evaporation combined with a scanty supply of fresh water causes rather high salinities, and, therefore, convection currents are limited to a very thin layer near the surface. In some isolated basins as the Red Sea, the Mediterranean and the inner part of the Gulf of California, however, they may reach to great depths, that is to the bottom itself (SVERDRUP, JOHNSON, FLEMING, 1946, p. 138, 147, 790). In the Mediterranean the nutrient content of the lower water layers is comparatively low; in the Red Sea it is, however, rather high and, therefore, the supply with nutrients by convection currents will be important.

Convection currents are of very great importance in temperate and especially in cold regions, where they penetrate to great depths. They occur in autumn and in winter; during that time the surface layers become rich in nutrients again. In winter light is the chief limiting factor for the production of the phytoplankton. As soon as in spring sufficient light and other favourable conditions are attained, a great phytoplankton production takes place. As a result the concentration of the nutrients diminishes rapidly, and as no renewal occurs before autumn, soon afterwards it is low again. Such areas are characterized by a great maximum in plankton production in spring (chiefly diatoms), a marked minimum in the production in the warmest time of the year, often to be followed by a secondary autumnal maximum (SVERDRUP, JOHNSON, FLEMING, 1946, p. 790).

2. UPWELLING WATER, turbulence, etc.

Upwelling is very important for the renewal of nutrients, and with that for the phytoplankton production. The effect of upwelling is more or less continuous throughout the year (SVERDRUP, JOHNSON, FLEMING, 1946, p.

727), or at least throughout that part of the year during which upwelling occurs. During that time the concentration of the nutrients remains high notwithstanding the great consumption by the phytoplankton. Therefore, in such regions a summer minimum due to exhaustion of nutrients does not occur. Most of the important regions of upwelling lie in the subtropics or in the tropics. In such regions light will be available all the year round in a sufficient amount to warrant a great production; and, therefore, a winter minimum due to lack of light does not occur either.

It has been demonstrated by HENTSCHEL (1928; 1933) and HENTSCHEL & WATTENBERG (1930), that the plankton production is very great indeed in the regions of upwelling near the coasts of SW and NW Africa; see further WATTENBERG (1928, 1937). The high production in the Peru Coastal Current has been demonstrated by GUNTHER (1936) and in the California Current by MOBERG (1928) and by SVERDRUP & ALLEN (1939). A high production occurs just as well in regions of ascending water lying far off the coast, for instance at the divergences in the vicinity of the equator (SVERDRUP, JOHNSON, FLEMING, 1946, p. 787), near the ridge between Cape Gardafui and the island of Socotra (GILSON, 1937), etc. However, as littoral conditions greatly favour the production (HART, 1942), the latter will be by far greatest in regions of upwelling lying near coasts.

In regions of "dynamically caused upwelling" (S coast of Africa, S coast of Florida, etc.), where deeper water layers occasionally ascend to the very surface, the supply of the well lighted water layers with nutrients and the production occasionally will be high too.

In the Antarctic region, where ascending water approaches, but does not reach the very surface, the supply with nutrients of the uppermost layers occurs only in the colder time of the year by convection currents. With the commencement of the new season the concentration of the nutrients diminishes rapidly as a result of the consumption by the phytoplankton. At the beginning of the season the quantity of the phosphates and of the nitrates was, however, so enormously great, that they are never depleted to such a degree as to become limiting factors for phytoplankton growth (HART, 1934*b*, p. 184; 1942, p. 273; shortage of silica probably may become a limiting factor). The production is, therefore, in the Antarctic region very high. A great production occurs, however, only during the very short southern summer, and, therefore, the total year production is probably much less than in regions of upwelling lying in low latitudes.

Turbulence also favours the renewal of nutrients, and its effect is also more or less continuous. Therefore, in regions where turbulence is important, a summer minimum due to exhaustion of nutrients does not occur. This situation occurs for instance in Puget Sound, where the nutrient concentration as well as the production of the phytoplankton are rather high from May until October (PHIFER, 1933, fide SVERDRUP, JOHNSON, FLEMING, 1946, p. 788). The effect of turbulence is, however, much less important than that of upwelling. Moreover, strong turbulence is on the other hand very unfavourable for a great production; the latter requiring a certain degree of vertical stability within the upper water layers.

Summarizing we may conclude: In cold and temperate regions the phytoplankton production is generally high in spring and sometimes in autumn as a result of convection currents. A minimum generally occurs in summer due to lack of nutrients; some regions of ascending currents (Antarctic, etc.) excepted. A winter minimum due to lack of light is always present.

In subtropical and tropical regions light is present all the year round in a sufficient amount to warrant a high production in the upper water layers; a winter minimum due to lack of light, therefore, does not occur. Still in those regions the production is generally very poor, because the supply with nutrients is very scanty, as convection currents are insignificant (some basins as the Red Sea excepted). A great production occurs, however, in those parts of the subtropics and the tropics where nutrients are adduced by ascending currents. The production is particularly high in regions of upwelling near coasts. In these regions cessation of production will occur also, but this must result from other factors than from lack of light or from depletion of nutrients. If in the tropics or subtropics upwelling occurs all the year round no marked minimum due to lack of light or of nutrients will occur in any season of the year. Therefore, it seems probable that in such regions the year production is nearly the highest on earth. According to GILSON (1937, p. 59) the productivity of the tropical upwelling areas exceeds that of any temperate sea. HART (1934*b*, p. 134) in claiming that the production in the Antarctic region is the highest on earth adds the following: "apart perhaps from such local effects as in the Benguella and Humboldt currents".

As animals live directly or indirectly on phytoplankton the number of animals is also very great in regions of upwelling. In the Peru Coastal Current the abundance of invertebrates, fishes and birds is astonishing (MURPHY, 1920, 1923, 1925; COKER, 1918, 1920; SCHOTT, 1932*b*; SCHWEIGGER, 1943). MURPHY (1923, p. 64) remarks concerning the coastal water of Peru: "the existence in littoral waters of a vast abundance of marine organisms, upon which are dependent in turn unsurpassed fishery resources, as well as the remarkable Peru guano industry". In the upwelling water along the coast of SW Africa invertebrates and fishes are also very abundant; only in the azoic zone several species of bottom feeding fish and particularly bottom living invertebrates are very rare. Other fishes, however, (plankton feeding!, etc.) may be very abundant. Great shoals of sardines for instance enter Walvis Bay year after year. The number of fish eating birds on this coast is also astonishing (VAN OORDT, 1940), giving rise to a guano industry; the deposition of guano in regions of upwelling being possible by the combined effect of very abundant bird life and the rainlessness of the coast region.

CHAPTER IX.

Upwelling water, red water of dinoflagellates and mass mortality of fishes and invertebrates.

In fresh water "waterbloom" of phytoplankton occurs particularly when the water is rich in nutrients. According to NAUMANN (1922) waterbloom is even an indicator for a eutrophic surrounding. In the same way in sea very dense populations of phytoplankton will occur particularly in regions that are rich in nutrients. Diatoms are very pretentious in their nutrient requirements. Therefore, a great production of these organisms is a good indicator, that the nutrient content is or shortly before has been high. As regions of upwelling are very eutrophic, conditions are highly favourable for a great production of this group. It has been demonstrated by MOBERG (1928) and SVERDRUP & ALLEN (1939) for the Californian coast that upwelling is reflected instantaneously in a large production of diatoms. In the same way the frequent occurrence of "dark water" caused by enormous masses of diatoms along the coast of SW Africa (see p. 18) must be related to the high nutrient content of the water and with that to upwelling. As upwelling occurs in this region in a varying degree all the year round, and consequently the concentration of nutrients is nearly always high, the diatoms will find suitable conditions during a great part of the year. A very high percentage of the yearly production of phytoplankton will, therefore, consist of diatoms.

With dinoflagellates matters stand somewhat different, as they are lovers of warmth. The distribution of this group is strongly influenced by temperature. In very cold regions they are poorly represented, although in antarctic regions they are not as scarce as was supposed formerly (HART, 1942, p. 271). In warm regions the plankton consists for a much greater percentage of dinoflagellates. According to KÄŞLER (1938) the distribution of the Dinophysiales (a group of the dinoflagellates) in the southern Atlantic shows an obvious relation with the distribution of temperature. For many species and genera of Dinophysiales the 15°—16° C year isotherme forms a marked boundary. Therefore, in the very cold water near the coast of SW Africa several species and genera do not find a suitable temperature. There are, however, genera of Dinophysiales and other dinoflagellates too, for which the low temperature of this region is not prohibitive.

Further the number of specimens of dinoflagellates is greatly influenced by temperature. In temperate regions they have their maximum in the warmer summer months (LEBOUR, 1925, p. 8). In the regions of upwelling at the coasts of SW Africa and Peru–Chile, where the negative temperature anomaly is very great, the temperature of the surface water is probably too low for great outbreaks of red water of dinoflagellates during a great part of the year; a suitable temperature for red water is probably attained only at certain occasions, when the upwelling is less pronounced and when warm water invades the very cold water near shore. In this respect the observation at the coast of Peru is important that red spots occur in those places where warm water invades the cool water of the Peru Coastal Current. Near Walvis Bay upwelling is minimal in December/January and as a result the water becomes much warmer in this time of the year (see p. 25); therefore, great outbreaks of red water will occur particularly in these months.

Dinoflagellates are much less pretentious in their nutrient requirements than diatoms, as they are able to reduce the nutrients in a higher degree and as owing to their mobility they are able to adjust themselves to the most favourable water level. Therefore, they will find optimal conditions at a lower nutrient content than diatoms, and hence even if the upwelling is less pronounced. PETERS (1934, p. 6) remarks with regard to the occurrence of the ceratiums (a group of dinoflagellates) in the southern Atlantic, that a great production of certain species of this group may occur in upwelling water which has been during some time at the surface.

Besides a sufficiently high temperature and a sufficiently high nutrient content obviously several other factors must be encouraging to produce a great abundance (see ALLEN, 1941). Calm weather with plenty of sunshine seems to be another essential. According to ALLEN (1946*a*) in every year of great prominence of dinoflagellates there has been calm weather and smooth seas for from two to five weeks. HORNELL (1917) and HORNELL & RAMASWAMI NAYUDU (1924) correlated the occurrence of red water at the Malabar coast with fine weather with plenty of sunshine.

In temperate regions nutrients are in most places nearly exhausted in the warmer time of the year. In tropical and subtropical regions the nutrient concentration is generally very low all the year round, with the exception of regions of upwelling and some other places (see chapter VIII). Therefore, it seems probable, that such regions are the obvious places for great outbreaks of red water and with that for mass mortality. Among these regions those of upwelling near coasts are by far the most important, and, therefore, outbreaks of red water so extremely dense as to cause mass mortality will occur particularly in such regions. Red water of holozoic dinoflagellates as *Noctiluca* will occur also in such regions, as these organisms feed on phytoplankton and, therefore, require nutrients indirectly. Further it is probable that paralytic poisoning of man by eating mussels or other invertebrates will occur particularly in regions of upwelling water. The latter phenomenon has been studied only in the California region of upwelling.

In table I the occurrence of upwelling water, red water and mass mortality is indicated (see further figs. 2 and 3 on pp. 20, 21). From this table it is evident that mass mortality in red water occurs at least in 3 of the 4 most important regions of upwelling: SW Africa, Peru and California. The occurrence of red water and mass mortality at the coast of S California has been connected already several years ago with the occurrence of upwelling water, for KOFOID (1911, p. 243) mentions that the local and periodical enrichment of the coastal waters of California "by the nitrogen bearing waters from the depth" is one of the primary causes for the occurrence of red water along this coast. However, as far as I am aware, the question whether this trio occurs in other regions of upwelling too, has never been put forward.

In the fourth of the most important regions of upwelling, NW Africa, mass mortality occurs also repeatedly; until now, it is, however, unknown whether this mortality occurs in red water.

Upwelling occurs along a great part of the coasts of Arabia (Red Sea, and also further along the Arabian coast to Cape El Hadd). It is, therefore, interesting that the name "Red Sea" was applied by ancient Greek authors to all coasts of Arabia (MONTAGNE, 1844, p. 361). At the Arabian side of the Southern part of the present Red Sea, where upwelling occurs in summer time, mortality in red water occurs in summer too; the nature of the red discoloration is, however, unknown. Between Aden and Perim, where upwelling occurs in summer, red water and mortality are reported to occur in summer too. It is, however, unknown if the mortality occurs in red water.

TABLE I.

Region of upwelling along the coast of (most important regions in italics)	Mass mortality occurs periodically or episodically	Mass mortality occurs in red water	Red discoloration is caused by dinoflagellates
1. *SW Africa*	+	+	+
2. *NW Africa*	+	?	?
3. Venezuela	+	?	?
4. Red Sea			
a. Arabian side	+	+	?
b. Southern part of Egyptian side	?	?	?
5. S. Arabia			
a. Perim–Aden	+	?	?
b. further east to Cape El Hadd	?	?	?
6. Somaliland south of Cape Gardafui	?	?	?
7. Ceylon	+	?	?
8. *Peru–Chile*			
a. Peru	+	+	+
b. Chile	+	?	?
9. *California*	+	+	+

The occurrence of red water and mortality in Gokasho Bay (Japan) has been connected by KOMAI (in: MIYAJIMA, 1934, p. 109) with the presence of the pearl oyster culture. By residues of the oysters being thrown in the bay the nitrate content of the water would be augmented, in this way creating favourable conditions for great outbreaks of red water. Red water occurs, however, not only in Gokasho Bay, but also in several other parts of the neritic waters of Japan.

As a result of local upwelling, turbulence, etc., the surface water around the islands of Japan is very eutrophic and, therefore, the phytoplankton production in many places is very high (see for instance KOKUBO, 1932; KIMURA, 1933; UDA, 1934; AIKAWA, 1936; KOENUMA, 1939, pp. 62 and 63). It remains to be investigated whether the occurrence of red water and mortality in Japan can be related with such oceanographical peculiarities.

In chapter IV it has been mentioned that along the southern coast of South Africa (region of the Agulhas Current) deep water occurs rather near to the surface; at some occasions (particularly in the southern summer) it ascends to the very surface. In this connection it is important that the periodical mortality near Knysna occurs (in the southern summer), when a narrow belt of cold water is present between the coast and the warm Agulhas water outside it (GILCHRIST, 1914); the direct cause of the Knysna mortality is, however, until now uncertain. A profile through the Agulhas Current near Saldanha Bay, showing "dynamically caused upwelling" is given in fig. 6 (p. 33); from this bay mass mortality is known to occur with certainty in red water.

"Dynamically caused upwelling" occurs also occasionally in the Straits of Florida. In future it must be investigated whether the occurrences of red water and mass mortality at the SW coast of Florida may be associated with this phenomenon or with local true upwelling.

HORNELL (1917) and HORNELL & RAMASWAMI NAYUDU (1924, p. 143) have correlated the high production of phytoplankton in the Malabar coastal water during the SW monsoon with a high nutrient content due to a great influx of river water in the rainy season. The high production season starts with a great development of diatoms in May. Some months later dinoflagellates and flagellates become very numerous; red water may appear from the end of August. "By this time the heavy and more or less regular daily rain that characterises the height of the south-west monsoon has abated, the sky is less overcast with cloud, and the sun once more becomes a power in the Malabar sky. But for long after the rains have decreased, the rivers continue to pour into the sea immense volumes of water laden with the drainage of the land and particularly rich in soluble nitrogenous material, chiefly nitrates, together with phosphates, and various other salts" (HORNELL & RAMASWAMI NAYUDU, 1924, p. 143).

The possibility is surely not excluded that the eutrophy of the coastal water may be the result of an influx of river water. However, other possibilities must be mentioned too. According to GILSON (1937, p. 57) by the stormy seas prevailing during the SW monsoon a certain amount of nutrients is probably adduced to the surface layers. The coincidence of a great production with the influx of river water is according to GILSON chiefly the result of the lowered salinity and consequently increased stability of the surface layers favouring the production.

A third possibility to explain the eutrophy of the Malabar coastal water is upwelling. According to GALLÉ (1928, p. 9) upwelling occurs along this coast during the SW monsoon between 6° and 10° N. On my inquiry, whether this situation occurs also somewhat more northerly Dr. H. KEYSER (De Bilt, Netherlands) informs me that this is the case indeed to about 14° N. The difference in temperature between the water near the coast and more offshore is not very great; therefore, it is not certain, whether these differences are indeed the result of upwelling.

Summarizing we may conclude: red water and mass mortality occur apparently in regions where a high concentration of nutrients is combined (at least during some time of the year) with a sufficiently high temperature. Therefore, red water and mass mortality occur in the high production areas of low and moderate latitudes and with that especially and in a very high degree in regions of upwelling; that is in very special areas characterized by various peculiarities. Regions of upwelling undoubtedly have existed in the geological past also; and, therefore, it is beyond question that great outbreaks of red water and with that mass mortality occurred also in other geological periods.

CHAPTER X.

Upwelling water and the peculiarities of the sediment of the azoic zone near Walvis Bay.

The peculiarities of the sediment of the azoic zone are:

I. The occurrence of a diatom ooze in a subtropical littoral part of the sea. II. The absence or great scarcity of remains of bottom living invertebrates. III. The abundance of fish remains. IV. The presence of H_2S and the high organic content of a sediment occurring in the open sea.

It will be shown that all these peculiarities owe their origin to the presence of upwelling water. When these peculiarities occur combined in a fossil deposit, the chance is, therefore, great that such a deposit originated in a region of upwelling water too.

I. DIATOM OOZE.

Diatom ooze is well known to occur in arctic and antarctic regions. Further it occurs generally in offshore positions only, where the supply with terrigenous material is scanty. The fact that in the azoic region a true diatom ooze occurs close to the coast in a subtropical latitude is, therefore, at first sight peculiar.

In the last decennia diatom ooze (or diatom mud) has become known except from the azoic region near Walvis Bay also from some other regions in comparatively low latitudes. It is a noteworthy fact that nearly all of these occurrences may be associated with upwelling water. This has been emphasized for the first time by W. SCHOTT (1936; see further W. SCHOTT in: G. SCHOTT, 1935 and 1942). The occurrence of diatom ooze in regions of upwelling water is connected by W. SCHOTT with the low temperature of these regions; a low temperature being unfavourable to most foraminifera and favourable to diatoms. The low temperature of regions of upwelling will have great influence on the composition of the plankton indeed, as most foraminifera prefer a high temperature, etc. The abundance of diatoms in the plankton, however, must be chiefly connected with the high concentration of nutrients, the temperature being of less importance. The high nutrient content in regions of upwelling is reflected particularly in a great production of diatoms (see p. 77). The amount of their skeletons sinking to the bottom will, therefore, be very great in these regions. A high abundance of diatoms is, however, not sufficient to produce a diatom ooze. Besides high abundance the following factors will be important:

1. Scanty supply with terrigenous material. The quantity of terrigenous material brought into the sea by rivers, rivulets, etc. is generally low as

a result of the rainlessness of the coast region; the rainlessness being caused in its turn by the presence of upwelling water (see chapter IV).

2. Scanty supply with and solution of a part of the calcareous organisms. The low temperature of regions of upwelling is unfavourable to most of these organisms. Further the carbon dioxide content of the lower water layers will be high as a result of the decomposition of a great amount of organic compounds, and this favours the solution of calcareous remains.

3. P_H. Some authors (PIRRSON, 1920, p. 433, fide STUBBINGS, 1939, p. 150 a.o.) have emphasized that diatoms are composed of silica in an insoluble form and are rarely destroyed. This is not correct. A very great part of the siliceous skeletons of diatoms is redissolved after death. This occurs particularly in those water layers, where the p_H is high (COOPER, 1933; CLOWES, 1938). In regions of upwelling the p_H generally will be high in the upper water layers as a result of the photosynthetic activity of the phytoplankton. Below the well lighted layers, the p_H is usually low due to the decomposition of a great amount of organic material, and the p_H is, therefore, unfavourable to the solution of siliceous remains.

Concerning the p_H of the sediment of the azoic zone near Walvis Bay COPENHAGEN (1934, p. 9) remarks: "The colorimetric determination gave figures of about 8. This question is being further investigated". This is desirable, for the p_H is remarkably high.

For the topographical relation between diatom skeletons and H_2S in the azoic zone see below.

4. Strong silicification in regions of upwelling? Diatoms that are not strongly silicified dissolve very easily. Only diatoms that are strongly silicified remain recognizable in bottom deposits (HART, 1942, p. 327). The occurrence of strongly silicified species, therefore, greatly favours the sedimentation of a diatom ooze.

According to COOPER (1933, p. 697) the occurrence of thick or thin walled species of diatoms appears to be a function of the amount of silicate present in the surface water: thick walled species being predominant when the amount of silicate is high, thin walled species being predominant when the amount is low. The observations by HART (1942, p. 324) on *Corethron criophilum* Castr. are also very suggestive in this respect; HART correlates the change over to a largely spineless, thinner walled form at a definite season with maximum depletion of nutrient salts and with that of silica.

If COOPER's suggestion holds good, upwelling water favours the sedimentation of a diatom ooze, because the content in silicates in the surface water is high, thus favouring the development of strongly silicified species or strongly silicified specimens of a certain species.

According to CLOWES (1938, p. 109) those diatoms have a good chance not to be redissolved of which the mortality is due to some cause other than being eaten by zooplankton.

The occurrences of diatom ooze in subtropical and tropical parts of the sea are of a rather small extent: narrow bands along the continents or little spots. They are, however, very important with regard to paleontology, because there are certain shales consisting for a great part of fossil diatoms, that according to their fish fauna have been deposited in near shore positions of relatively low latitudes too (menelite shales, Monterey shales, etc.).

A diatom ooze does not occur in all regions of upwelling, but only in parts of some regions, where the circumstances are very favourable (supply of terrigenous material particularly scanty, etc.). In the region of upwelling at the coast of California, as far as I am aware, no diatom ooze is formed in recent time, but it has been deposited in these latitudes in the geological past at more than one occasion (miocene, etc.). It is obvious that already a small change in the circumstances (e.g., a little change in the direction or the strength of the prevailing winds) will be decisive as to whether or not a diatom ooze will be formed.

The following occurrences of diatom ooze (or mud) are known:

a. Antarctic circumpolar. A virtually continuous band of diatom ooze occurs around Antarctica. Several authors (W. SCHOTT, in: G. SCHOTT, 1935, p. 119, and W. SCHOTT, 1936; MACKINTOSH, 1946) have pointed to the fact that the northern boundary of this band coincides nearly exactly with the Antarctic Convergence.

b. In the Arctic a band of diatom ooze occurs in the Pacific only. Following the Oya Shio it stretches as far south as 37° N. According to W. SCHOTT (in: G. SCHOTT, 1935, p. 118) the southern boundary of the diatom ooze coincides with that between the Oya Shio and the Kuro Shio and, therefore, with the Arctic Convergence.

c. A narrow band of sediment, in which diatoms are very abundant, occurs along the west coast of S America nearly between 2° and 36° S (MURRAY & LEE, 1909: NEAVERSON, 1934); this sediment contains a fair amount of terrigenous material, and, therefore, it is classified by NEAVERSON as diatomaceous mud. The diatom debris are usually sufficient in quantity to impart a green colour to the mud; the green colouring matter appears to be due to the presence of chlorophyll.

d. Azoic region near Walvis Bay. The sediment in this region is not a diatom mud, but a true diatom ooze (PRATJE, 1939). Near the coast of SW Africa the rainlessness is very pronounced. The rivers carry water on rare occasions only; therefore, the amount of terrigenous material brought into the sea by these rivers is during long intervals practically zero. Moreover it is of great importance that sand transported by wind is not blown far out over the sea in this region (in contradistinction to the situation near the coast of NW Africa, see p. 28). Hence, the sedimentation of a true diatom ooze close to the coast has been possible.

According to STEER (in: COPENHAGEN, 1934, p. 16) the majority of the diatoms are *Coscinodiscus* and *Actinocyclus* spp.

e. Arabian Sea. According to STUBBINGS (1939) the siliceous skeletons of diatoms occur rather seldom in sediments of the Arabian Sea. They are, however, common in sediments off the mouth of the Gulf of Aden (in the vicinity of Cape Gardafui) and they are even very abundant in green mud occurring off Cape El Hadd (SE Arabia). The occurrence of diatom frustules in the sediments of the Arabian Sea is correlated by STUBBINGS (l.c., p. 151) with increased productivity due to the transport of nutrients to the surface by upwelling water along the African and Arabian coasts during the SW monsoon.

The predominating diatoms found in the sediments of the Arabian Sea are *Coscinodiscus* spp.; at Cape El Hadd the diatoms are all of the species *Coscinodiscus oculis-iridis* var. *borealis* (Bail.), Cl. Apparently this is the only species that is so strongly silicified that it does not become dissolved. At station 55 of the John Murray Expedition (SEWELL, 1935), where diatoms occur in large numbers, the sediment is very near to a true diatom ooze.

f. Pacific, east of the Philippines. FLINT (1905) described a deep sea deposit of which the principal constituents were the frustules of diatoms from 14° 28′ — 14° 50′ N, 130° 0′ — 130° 30′ E. HANZAWA (1936) described a number of diatom oozes from nearly the same region. They formed relatively small areas, as they were interrupted by areas of globigerina ooze and red clay. The predominating diatom was *Ethmodiscus* sp. The patches found by HANZAWA occurred within the area 19° 8.5′ N to 8° 40′ N, 136° 32.6′ E to 153° 6.5′ E.

g. Southern Indian Ocean midway between Madagascar and Kerguelen, about 38° S (MURRAY & PHILIPPI, 1908).

It seems probable that it will turn out that f and g can be related with a high nutrient content of the surface water and hence with the ascending of deeper water layers too.

II. Scarcity of remains of bottom living invertebrates in the sediment of the azoic zone.

The scarcity of these remains will be chiefly the result of the fact that live specimens are very scarce too.

Red water is very injurious to various groups of invertebrates. In regions where red water occurs repeatedly a great part of the benthonic fauna will be gradually exterminated. After heavy occurrences of red water H_2S is apparently present for a short time in the free water (see below): the presence of H_2S will be very noxious to the invertebrates living in and on the sediment, and their number will be greatly diminished by this factor too.

After a catastrophe the benthonic invertebrates will try to regain the lost territory from all sides. They are, however, for the greater part slow moving creatures; therefore, most of them will not have penetrated into the azoic zone very far, when a new catastrophe occurs. Moreover it will be difficult for them to regain a territory where the sediment is strongly impregnated with H_2S. Their pelagic living larvae, however, will soon be present again; CLASSEN (1930) mentions, that very young mussels enter the water of Walvis Bay every year to be nearly completely exterminated again and again.

III. Abundance of fish remains in the sediment of the azoic zone.

In contradistinction to benthonic invertebrates various species of fish are quick moving animals. These will be able to regain the whole territory in a rather short time after the catastrophe, to be massacred again, if a new catastrophe occurs.

According to MARCHAND (1928) fish remains are very abundant in the sediment of the azoic zone; when trawling fish bones may be brought up by the bucketful.

In recent marine sediments remains of fish are usually very scarce; deep sea deposits are especially deficient in this respect. Otoliths and isolated teeth are the only fish remains that occur rather frequently, but the softer bones like the vertebrae and the ribs fail nearly completely (ANDRÉE, 1920, p. 405; MURRAY & CHUMLEY, 1924, p. 248). In the shelf sea remains of fish are usually rare too.

There are, however, marine fossil deposits in which fish remains occur in great quantity. SMIRNOW (1930, p. 363) in dealing with the fauna of the oligocene of the northern Caucasus mentions, that this deposit looks like a graveyard of fish. In other bituminous shales (menelite shales of the Carpathians, Monterey shales, Kupferschiefer, etc.) fish remains occur in great quantity too. In such sediments besides isolated parts of fish often nearly complete skeletons are to be met with. Because such deposits originated in the geological past, it is of importance to search for an analogon in recent time. Therefore, it is worth while to study the few recent sediments where fish remains occur in great quantity (azoic region near Walvis Bay and Cape El Hadd; Bay of Talcahuano; probably also in parts of other regions of upwelling: Bay of Callao, Peru?).

Now the question arises, whether ultimately something will be preserved of these fish remains, and if so in what state of preservation. In the sediment of the Bay of Talcahuano nearly complete fishes were observed by FALKE (1939) several months after the mortality.

For a good preservation of fish remains a quick embedding after death is a first requirement. The latter is possible in two ways: either they are covered directly after death with a rather thick layer of sediment or they sink away in a soft sediment in which anaerobic conditions prevail. It is possible that the fish are covered nearly directly after death with a thick gelatinous mass of dinoflagellates that have passed into the jelly forming resting stage (see p. 44); or by dinoflagellates that died shortly after the plankton maximum. By the blanketing effect of this gelatinous mass they will be shut off, at least provisionally, from oxygen bearing water and probably will be prevented to rise to the surface. Secondly the fishes will partly sink away in the soft green mud. As will be emphasized below, this mud is probably near to a true sapropelium. The pappy mass of a sapropelium is an ideal surrounding for the preservation of fish remains. POTONIÉ (1908, p. 133) remarks in this respect: "Die figurierten Konstituenten sind nun in den bereits homogen zersetzten Hauptmasse gewissermassen eingelegt wie ein zu konservierendes mikroskopisches Präparat in Glyzerin, Spiritus oder dergl." Further POTONIÉ (1908, p. 139) remarks: "Die ordentlich gefaulte Masse hüllt die schneller niedersinkenden Teile ein, die so dem wenigen Sauerstoff, der eventuell am Grunde des Wassers vorhanden ist, ganz entzogen werden. Dadurch zeigen sich gewisse figurierte Bestandteile, sogar ganze Organismen, so oft noch in trefflicher, dauernder Erhaltung."

It seems, therefore, highly probable that fish are fossilized in regions of upwelling, i.e., in those parts of these regions, where a sediment occurs that is near to a true sapropelium. During red water outbreaks invertebrates (cephalopods! etc.) and vertebrates other than fish (e.g., aquatic reptiles: turtles and sea snakes, see p. 66) perish also. In the present time aquatic reptiles are not abundant in most of the regions of cold upwelling water. In those regions, however, where they are abundant, or in those geological epochs in which they were abundant, remains of such animals will sink away in the soft sediment in a considerable number, and will thus become fossilized.

It is probable that besides aquatic vertebrates shore dwelling terrestrial vertebrates eating of the poisoned fish, clams, etc., will perish within a very short time (see p. 66). These terrestrial vertebrates also have a chance to become fossilized, if their remains are washed into the sea during high tide.

IV. H_2S and high organic content.

With regard to the presence of H_2S and the high organic content the following is important:

a. Great production of organisms. The abnormally great production in regions of upwelling, particularly in those where upwelling occurs all the year round, has been emphasized in chapter VIII.

b. Low temperature of the surface water. The comparatively low temperature of the surface water in regions of upwelling is important as it delays bacterial action, and with that the decomposition of the organic remains on their way to the bottom.

c. Distance from the coast. The longer the time until the bottom is reached the more organic matter will be decomposed. If the water is very deep, a high percentage of the organic compounds is oxidized long before reaching the bottom. Now several authors (KRECJI, 1936*a*, p. 63, a.o.) have emphasized that the organic compounds will be oxidized likewise in shallow water near the coast (at least as far as the open sea is concerned), because light plankton organisms can hardly settle permanently on the bottom in the agitated water of such regions.

The organic sediment of the SW African coast occurs in the somewhat sheltered Walvis Bay (probably also in a part of Great Fish Bay, see below) and further in the open sea. With regard to the occurrence in the open sea it is, however, remarkable that there exists a narrow strip (about 3 miles wide) between the azoic zone and the coast where the bottom consists of grey sand, and where it apparently does not contain hydrogen sulphide gas (COPENHAGEN, 1934, p. 6). Probably in this region the water is too turbulent for a high production, as well as for a quiet sedimentation, but somewhat more offshore the water is apparently sufficiently quiet for a high plankton production and for subsequent deposition of large amounts of organic matter (see fig. 1; at Sandwich Harbour lying within the sandy strip mass mortality occurs on rare occasions only).

d. Position of discontinuity layer.

At the end of their life phytoplankton organisms mostly sink to deeper water layers to die when arriving below the compensation depth (= the depth where the oxygen consumption by respiration equals the oxygen production by photosynthesis, SVERDRUP, JOHNSTON, FLEMING, 1946, p. 779). Therefore, the dead organisms are already below the most agitated layers, when decomposition begins.

After death the remains continue to sink, often accumulating at a certain depth, where there is a marked increase in the density of the water; in this discontinuity layer the greater part of the organic matter is decomposed. However, if a marked discontinuity at the lower limit of the productive zone is absent, there is no tendency for an accumulation at any water level.

In regions of upwelling the discontinuity layer fans out towards the surface (fig. 4 on p. 24). At the coast of SW Africa it rises gradually from west to east to about 0 m at the coast (DEFANT, 1936). Therefore, there is a zone along the coast where there is no marked increase in density below the depth, where the plankton dies. This situation affects the rate of sinking of the dead plankton.

e. Influence of plankton maxima and mass mortality on the oxygen content of the lower water layers.

In regions of upwelling where the production of plankton and with that the amount of dead plankton sinking to the bottom is very great, the oxygen content of the water below the euphotic region becomes low. It will be very low, and carbon dioxide will be produced in a considerable quantity after times of plankton maxima, and particularly when the latter are accompanied by mass mortalities. In years of limited mortality the effect of the dead fish on the oxygen content of the lower water layers will be local only; in years of great mortality, however, the millions of dead fish (sinking to the bottom either directly or after having floated for some time) will greatly affect the oxygen content of these layers.

After times of red water and mass mortality an enormous mass of organic material sinks to the bottom in a very short space of time. By the decomposition of a fraction of this enormous mass the oxygen content in the sediment, and probably also in the free water (lower layers) will be exhausted. Under such conditions sulphate reducing bacteria multiply and produce considerable quantities of H_2S: It is well known from some places along the coast of Peru that the red water occurrences may be followed by a development of H_2S, blackening the paint of ships, etc. (see p. 52). Therefore, after pronounced occurrences of red water H_2S is apparently present for some time in the free water. In the Bay of Talcahuano (where an occurrence takes place annually that is probably very similar to that at Walvis Bay, see p. 61), H_2S occurs in the free water in some places during a great part of the year, in other places only during some time after the phytoplankton maximum that is accompanied by a great mortality (FALKE, 1939). This applies, however, to conditions in a bay. It seems unlikely that in the open sea H_2S will be present in the free water for a long period.

f. Organic nature of the sediment.

As a result of the great production combined with a scarce supply of terrigenous material the sediment consists for a very high percentage of organic remains, and with that chiefly of soft, unicellular plankton algae; therefore, it will form a gelatinous, colloidal mass. Such a mass is nearly impervious to water. Therefore, it seems probable that O_2 cannot penetrate into the sediment, even if some O_2 is again present in the lowest water layers some time after the plankton maximum.

According to MARCHAND (1928, p. 2) in all cases where dead diatoms occur in the bottom samples of the azoic region the sulphur test is positive and where they are absent the test is negative (see also the sediment near Cape El Hadd, p. 94). In this respect it is interesting that COPENHAGEN (1934, p. 9) mentions the following: diatoms appear to possess a selective absorption for sulphuretted hydrogen. From an experiment by this author it would appear that the diatomaceous mud absorbs and holds this gas.

It is also possible that the connection between H_2S and diatoms must be explained in the following manner: both may be connected with the decomposition of organic matter (see page 83: sub 3).

g. Scarcity or complete absence of benthonic invertebrates. The extermination of these organisms favours the anaerobic condition within the sediment; for they are the scavengers of the sea bottom, while burrowing they digest the organic matter, and further they bring oxygen bearing water to deeper layers of a sediment.

By the organic nature of the sediment, and moreover by the scarcity of benthonic invertebrates it seems possible that anaerobic conditions once prevailing in the sediment may continue even in the open sea.

In this way it seems probable that even in the open sea a considerable part of the organic compounds is preserved in a reduced form. The organic matter occurring in the sediment will surely not consist only or even not chiefly of remains of red water plankton and of fishes, but will be a percentage of all the organic material sinking to the bottom throughout the year; amongst this material diatoms will play an important part.

The principal factors that cause the origin of H_2S and the high organic content are, therefore: 1. Abnormally high annual production of plankton and other organisms; 2. Relatively low temperature of the surface water; 3. Red water and mass mortality of fishes and invertebrates; 4. Scarce supply of inorganic material. As in last instance all these factors are the result of upwelling water, the H_2S and the high organic content owe their origin to the presence of upwelling water too.

TRASK (1932; see also TRASK, 1939, p. 446) has correlated the rather high organic content of some sediments near the coast of Southern California with the great productivity of regions of upwelling. WISEMAN & BENNETT (1940) did the same with regard to sediments in some coast regions of the Arabian Sea. CORRENS (1937, p. 236) found the same correlation in the surroundings of the Cape Verde Islands. However, sediments with a very high organic content, and in which H_2S is present in great quantity, occur in parts of regions of intense upwelling only. They occur in those parts of these regions where the accumulation of organic material on the sea bottom is abnormally high, particularly at certain times of the year (waterbloom and mortality), and where the decomposition of this material by aerobic organisms is relatively small (azoic areas: benthonic invertebrates nearly absent). As a result the decomposition by aerobic organisms can in no way keep pace with the supply of organic material, and therefore, a great part of the organic compounds is converted by anaerobic bacteria only and is preserved in a reduced form.

The conception that a large production is of chief importance for the origin of a marine sediment with a high organic content has been disputed by several authors, e.g., by KRECJI (1935*a*, 1935*b*, 1936*a*, 1936*b*, 1936*c*, 1938). This author repeatedly emphasized that a high plankton production does not suffice to warrant that the quantity of organic material being ultimately preserved will be high too. For the ultimate preservation it is according to KRECJI much more important, that the environment is unfavourable for the destruction of the organic compounds. Most authors agreed with this argumentation, and, therefore, petroleum geologists are nowadays not so much in search of a correlation between sediments with a high organic content and regions of great production, as of a correlation between such sediments and factors preventing decomposition by aerobic organisms.

In parts of regions of very intense upwelling, where the aerobic decomposition cannot keep pace with the supply, anaerobic conditions prevail within the sediment, and therefore, factors preventing the destruction of organic compounds are surely present. The anaerobic condition is not the result of a topographical, but of an oceanographical peculiarity (upwelling). Therefore, the importance of upwelling for the origin of a sediment with a high organic content is twofold: firstly it causes a high production, and secondly it causes to develop factors preventing the oxidation of the organic compounds.

KRECJI emphasizes that as the production is higher, the number of the scavengers of the sea bottom, mainly benthonic invertebrates, is proportionally higher too. This is indeed generally the case. SVERDRUP, JOHNSON, FLEMING (1946, p. 893) mention in this respect: "The concentration of detritus feeders is, of course, dependent upon the extent of production of plants and nonscavenger animals. Where this production is great, there also the scavengers must be numerous." In some parts of regions of upwelling, however, where the production is extra-ordinarily great, benthonic invertebrates are nearly absent.

Which of both is the sediment of the azoic zone near Walvis Bay, gyttja or sapropelium? The presence of H_2S in a sediment is certainly no proof that it is a sapropelium, for in the deeper layers of gyttja H_2S occurs just as well. The issue is, where the boundary O_2/H_2S is to be met with (WASMUND, 1930; see further the papers by KRECJI cited above). In gyttja this boundary lies at some distance below the surface of the sediment. Because O_2 is present in the superficial layers of gyttja the greater part of the organic compounds is lost during their stay in these superficial layers by the destructive action of aerobic bacteria or of burrowing invertebrates. In gyttja the greater part by far of the organic compounds, therefore, is lost, before they are covered with a sufficiently thick layer to come out of reach of burrowing invertebrates and of oxygen bearing water. In sapropelium the boundary O_2/H_2S does not lie some distance below the surface of the sediment, H_2S being present to the topmost layer. According to WASMUND (1930) the boundary must lie in the free water. Consequently O_2 cannot penetrate the sediment and benthonic invertebrates cannot live in or on the sediment, the decomposition of the organic material occurring under influence of anaerobic bacteria only. Hence the organic compounds are not lost, but are preserved in a reduced form; even labile organic compounds (albumens, chlorophyll!) are not destructed. According to FALKE (1939) part of the sediment of the Talcahuano Bay must be considered as a true sapropelium. As H_2S occurs in parts of the bay in the free water during a great part of the year, in other parts at least during some time, the requirement for sapropelium that the boundary O_2/H_2S must lie in the free water is fairly well fulfilled at Talcahuano. The azoic zone of SW Africa occurs, however, except in Walvis Bay itself, also in the open sea beyond; for the latter region it is improbable, that WASMUND's requirement is fulfilled during a long time. On the other hand, as the organic content of the sediment is considerable, it is also improbable that the boundary lies far below the surface, for in that case by far the greater part of the organic compounds would have been destroyed during the stay in the uppermost layers. A sharp distinction between gyttja and sapropelium cannot always be drawn in nature. There are transitional stages, one being nearer to gyttja, the other to sapropelium (WASMUND, 1930, p. 337). At any rate the sediment of the azoic zone is not a typical gyttja; a character of the latter being the presence of benthonic invertebrates (KRECJI, 1935*a*, p. 206). As the latter are nearly absent in the azoic zone, a great part of the sediment will be converted by bacterial action only. A part will be converted by aerobic bacteria (especially in places where there is a rather strong movement of the lower water layers, so that the sediment is churned up) and, therefore, will be destroyed; another part, however, will be converted by anaerobic bacteria only.

Therefore, it seems probable that the sediment of the azoic zone (at least parts of it) is rather near to a sapropelium, while at various places transitional stages to gyttja will occur. The organic compounds will surely not be preserved as completely as in the Black Sea sapropelium. However, in regions of upwelling the supply is so enormous, that even if the economy is less great, the residue will still be considerable.

According to STRØM (1939) the sediment of the azoic zone near Walvis Bay is not important with regard to the origin of "black shales", as its colour is not black but dark green. Sediments deposited under H_2S containing bottom water always have a black colour according to this author. KUENEN (1943, p. 28) has, however, emphasized that this is incorrect. The sediments of Kaoe Bay (Halmaheira, East Indian Archipelago, see VAN RIEL, 1932; KUENEN, 1939, 1943; NEEB, 1943) are also green, while it is known with certainty that they are deposited under H_2S containing bottom water. The green colour of the sediment of the azoic zone near Walvis Bay is, therefore, no proof against the conception that this sediment is near to a sapropelium.

In fresh water sapropelium may originate either by stagnation of the lower water layers or by an abnormally great supply with organic material (WASMUND, 1930). KRECJI (1935*b*, p. 75) is of the opinion that a marine sapropelium may originate by stagnation of the lower water layers only. TWENHOFEL (1939) and STRØM (1939) are less decided in their assertion that other possibilities are wholly excluded; both admit that on rare occasions a sapropelium may originate in the open sea owing to a great supply with organic material. However, these authors are also of the opinion that stagnation is by far the most important cause of the origin of recent marine sapropeliums as well as of black shales. As stagnation does not occur in the open sea there should always be some topographical peculiarity (a threshold or a depression in the sea bottom or something alike) to enable the origin of a marine sapropelium. In the present time stagnation occurs only in basins [1] of rather small extent (some fjords and bays with a threshold at their entrance) or in basins the origin of which requires circumstances that are only rarely attained (Black Sea). Several authors (KRECJI, 1935a, p. 206; WATERSCHOOT VAN DER GRACHT in: WOOLNOUGH, 1937, p. 1115; STRØM, 1939, p. 368, etc.) are, therefore, adherents of the hypothesis that the bottom water of the ocean stagnated under another climate than is present on earth nowadays, on account of the absence of polar ice caps; under such circumstances a sapropelium could come into being in the open sea.

If the sediment of the azoic zone near Walvis Bay by a further analysis (exact estimation of the organic content not only of the upper but also of deeper layers; labile organic compounds preserved?, etc.) is shown to be near to a sapropelium, proof would be furnished that under present climatic conditions a sapropelium of several thousand square miles may originate in the open sea without any water stagnation. It must be admitted that topographical factors surely may favour the anaerobic situation. The rather quiet conditions in bays (these need not to be bays with a threshold at the entrance) favour such a situation indeed; moreover, quiet conditions are favourable for a mass development of phytoplankton and with that for the development of red water and mass mortality. Therefore, the sapropelium like sediment will occur particularly in sheltered bays of regions of upwelling. It is, however, surely not limited to semiseparated parts of the sea, for it does not require complete stagnation of the lower water layers, but only moderate turbulence. Therefore, it occurs also in the open sea, probably in general somewhat further offshore.

Finally the question must be answered if sediments similar to that of the azoic region near Walvis Bay occur in parts of other regions of upwelling also. Until now exact data are scarce and unfortunately most of these refer to bays. With regard to the Great Fish Bay (most northern part of the region of upwelling near SW Africa) CHUN (1903, p. 142) remarks that in the head of the bay the enormous amount of organic material accumulating on the bottom is not fully consumed. The sediment has a very unpleasant odour of putrefaction, whereas the bottom fauna is poor. The organic content of this sediment is unknown to me. A similar sediment may be expected in (parts of) other bays on the SW African coast.

The sediment of the Bay of Talcahuano (southern part of the region of upwelling at the coast of S America) has to be considered in part as a true sapropelium (FALKE, 1939). It is unknown to me if an azoic zone occurs

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[1]) "Oceanographically a basin is defined as a depression that is filled with sea water and that is partially separated by land or submarine barriers from the open ocean, with which horizontal communcation is restricted to depths less than the greatest depths in the basin." (SVERDRUP, JOHNSON, FLEMING, 1946, p. 147). It must be emphasized that stagnation does not occur in all basins, but only under certain climatical circumstances (Ibidem, p. 148).

anywhere in the open sea in this region or in the northern part of this region of upwelling (coast of Peru). All I know of the latter region is that the sediment of the Bay of Callao is strongly impregnated with H_2S.

Region of upwelling along the SE coast of Arabia: SEWELL (1935, p. 5; see also 1934, p. 86) remarks the following with regard to this coast: "we further discovered the existence of a zone between the depths of some 100 metres and 1300 metres in which there seems to be a complete absence of life, though above and below there is a varied and in places a rich fauna; throughout this area the bottom consists of a soft green mud, that in the neighbourhood of Cape El Hadd is strongly impregnated with sulphuretted hydrogen gas". Moreover a slight trace of H_2S was detected by the John Murray Expedition in a bottom deposit of green mud obtained at a depth of 95 metres on the Arabian coast in 13° 51′ 30″ N, 47° 49′ 12″ E (station 189) in the Gulf of Aden. SEWELL (1934, p. 688) remarks with regard to this occurrence: "and this possibly represents a western extension of the conditions found to be present farther to the east off Cape Ras-al-Hadd".

LEES (1937) supposes that the occurrence of H_2S in the sediment near Cape El Hadd is an analogon of the situation in the Black Sea, and, therefore, that it is caused by stagnation of the lower water layers behind some barrier. TWENHOFEL (1939, p. 1196) is of the same opinion. As upwelling occurs along this coast eastward as far as Cape El Hadd it seems probable (as I have emphasized in some preliminary papers, BRONGERSMA, 1944, 1947*a*, 1947*b*) that the H_2S near Cape El Hadd (and also in the Gulf of Aden) has a similar origin as near Walvis Bay, that is an abnormally high supply of organic matter. Further it is important that the organic content of the sediment near Cape El Hadd is high (WISEMAN & BENNETT, 1940). Moreover, the sediment near Cape El Hadd containing H_2S consists for a great part of fish remains (scales, bones, etc.); only some of the samples consist for a high percentage of the siliceous frustules of diatoms (cf. STUBBINGS, 1939).

CHAPTER XI.

A possible explanation of the frequent occurrence in close proximity of petroleum and salt.

In has been shown in the former chapter that upwelling may have a marked influence upon the sediment of the littoral sea, leading in some cases to the deposition of a sediment that has much resemblance with a true sapropelium. Moreover, upwelling water has a marked influence upon the climate of the coast region, causing in some cases even complete rainlessness of the hinterland (chapter IV). Therefore upwelling may lead to a combination of two quite different sediments: a sapropelium like sediment in the sea, and sediments testifying of a very dry climate on and along the land. As upwelling must have occurred in the geological past too, the question arises if such a combination also occurs among fossil deposits.

To go into this problem in detail is beyond the scope of the present paper. However, the following short remarks may be offered: As a result of the close association often existing between petroleum and salt, early investigators proposed a hypothesis of a genetic relation between these two products. The well known opinion of OCHSENIUS (1891) was: "Kein Petroleum ohne salzige Gesellschaft". In the present time this hypothesis of a genetic relation does no longer find adherents. Still it is a fact (MACOVEI, 1938, p. 64) that at least in some cases there is a topographical relation between source beds of oil and sediments testifying of a very dry climate, inter alia salt.

This topographical relation is explained by MACOVEI in the following way: Petroleum originates according to this author under basin conditions. MACOVEI emphasizes that the relation between petroleum and salt is a mere relation of succession in the formation of two products under basin conditions: firstly the source sediment of petroleum and afterwards (when the basin was semiclosed) the salt.

It is not excluded that the topographical relation (at least in some cases) may be explained in another way:

Between the sediment of the azoic region near Walvis Bay and the salt deposits along the coast there is no genetic relation whatever, the two originating quite independently of each other. Neither does the relation exist, that both are deposited under basin conditions (for a great part of the sediment of the azoic zone is deposited in the open sea). The only relation between them is that both are the result of upwelling water: the sapropelium like sediment of the azoic zone being deposited in the open sea as well as in the bays along the coast as long as the salt concentration is rather normal, and the salt being deposited in the bays under the excessively rainless climate of the coast region as soon as the bays are semiclosed and the salt concentration becomes very high.

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SUMMARY.

The object of the present paper is to emphasize the importance of upwelling water to oil geology and to vertebrate paleontology. The study starts from the remarkable similarity existing between a sediment occurring in the Walvis Bay area (SW Africa) and bituminous fish shales. This similarity is particularly striking with those shales that consist for a high percentage of the siliceous frustules of diatoms (or of siliceous material deriving from these frustules): Californian miocene Monterey shales, oligocene menelite shales of the Carpathians, Caucasus, etc. These shales are considered by most authors as source beds of oil. It is explained that all the peculiarities of the sediment near Walvis Bay (diatom ooze, high organic content, H_2S, abundance of fish remains, great scarcity of remains of benthonic invertebrates) are caused in the last instance by upwelling water. If the same combination of peculiarities occurs in a fossil deposit, it is probable that this deposit originated also in a region of upwelling. Such sediments do not occur throughout regions of upwelling, but only in those parts of these regions, where the decomposition by aerobic organisms can in no way keep pace with the supply of organic matter.

To explain the connection between upwelling water and the peculiarities of the sediment near Walvis Bay, the mass mortality that nearly every year occurs in this region is discussed. Contrary to the general opinion that the mortality is caused by H_2S, I arrive at the conclusion that it is caused by noxiousness of red water of dinoflagellates (probably a poison produced in the living plankton). From a study of the literature on red water and mass mortality, and from inquiries to persons living in regions of upwelling, it becomes evident that these phenomena occur in nearly all of these regions. If upwelling is very intense (SW Africa), red water and mass mortality occur very often and in a very high degree.

The annual organic production in the subtropical and tropical upwelling water areas is among the highest on earth. Consequently the amount of organic remains sinking to the bottom is rather high. In parts of regions of upwelling, where a mass development of plankton ("dark water" caused by diatoms; "red water" caused by dinoflagellates, etc.) occurs repeatedly, the accumulation on the sea bottom is very high at certain times of year. It is particularly high if the occurrences of red water are accompanied by great mass mortalities. By these mortalities not only vertebrates (chiefly fish), but also benthonic invertebrates, the scavengers of the sea bottom, perish. If the mortalities occur very often, these animals become nearly exterminated. In these areas the decomposition by aerobic organisms is relatively poor. Consequently the decomposition cannot keep pace with the supply, and a great part of the organic compounds will be

converted by anaerobic bacteria only, and will be preserved in a reduced form. Hence it seems probable that a sediment that is rather near to a true sapropelium may originate in the open sea.

Remains of fishes that perished during mass mortalities have a good chance to become fossilized, at least in those regions where the above mentioned sediment occurs. If the fish partly or wholly sink away in the soft sediment, in which anaerobic conditions prevail, they will be shut off from oxygen very soon after death. Hence they come under very favourable conditions for preservation.

As it is shown in the present study that the mass mortalities as well as the sediment are the result of the presence of upwelling water, the regions dealt with are of importance to vertebrate paleontology. They show us fossil deposits, rich in vertebrate remains, in statu nascendi.

Upwelling water has a marked influence upon the climate of the hinterland, causing in some cases even complete rainlessness of the coast region. Consequently upwelling may lead to a combination of two quite different sediments: a sapropelium-like sediment in the sea, and sediments testifying of a very dry climate (e.g., salt) on and along the land. Such a combination occurs also among fossil deposits.

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