CHAPTER XIX

Organic Production in the Sea

In the previous chapters dealing with the marine organisms in relation to the factors of the inorganic and organic environment, we have had many occasions to refer directly to plant or animal production in the sea. Indeed, most biological studies relating to controlling factors lead to and are essential to an elucidation of the problem of quantitative and qualitative production of plants or animals in the sea. Studies pertaining to production in the sea are of vital interest to several marine sciences, particularly to the chemical, biological, or geological, because of their bearing on the extent, time, and spatial distribution of organic and certain inorganic constituents of the water and of the bottom.

The *gross production* (primary production) in the sea can be defined as the amount of organic material which by the activity of organisms in unit time is synthesized in a unit volume of water (production per unit volume), or in unit time is synthesized from inorganic substances in a water column of unit area cross section and extending from the sea surface to the bottom (production per unit area). The amount of organic material can be expressed as carbon, and thus, the production per unit volume can be reported as grams of carbon per cubic meter per day and the production per unit area as grams of carbon per square meter per day (daily gross crop). *Productivity* of the sea, on the other hand, can be defined as the capacity to produce, and is commonly used as a qualitative term for indicating the fertility of any ocean region.

The term production is also frequently applied in a more limited sense, namely, to denote the *product*, that is, the amount produced, of any given group of organisms in the sea. The terms plant production, phytoplankton production, zooplankton production, and commercial production are thus employed. The plants are the only organisms in the sea which can synthesize organic matter from inorganic substances in significant quantities. The *plant production*, therefore, nearly equals the gross production minus the amount of organic matter that is oxidized by the plants themselves and the amount that is secreted by the organisms. Where the depth to the bottom is too great to permit the existence of attached algae, the phytoplankton comprises all plants and the *phytoplankton production* equals the gross production minus the organic matter that is oxidized by the phytoplankton itself or is secreted. The phytoplankton production can be reported as grams of carbon per cubic meter per day, or per square meter per day, or as wet plankton or dry plankton (p. 928). *Zooplankton production* is the amount of digested material that is converted into animal protoplasm; that is, zooplankton production represents the difference between the amount of digested food, both plant and animal, and that used in katabolic processes. The *commercial production* is a term which is applied to marine products of commercial value. It might be defined in a similar manner, but usually the commercial production is measured by the yield of fishing and harvesting operations. However, this yield is not a true measure of the production because it also depends upon the intensity of the fishing and the gear used.

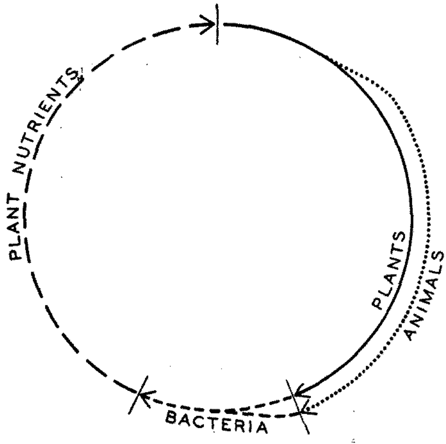

Fig. 248. The cycle of organic matter in the sea.

It is necessary to distinguish sharply between *production* and *population*. Population is the amount of organisms per unit volume or unit area as given by weight (grams of carbon, dry weight, or wet weight) or by number present at any given time. The populations can therefore be ascertained by a single survey, but in order to determine the production at least two surveys must be made at different times, and the processes must be known by which organic matter is built up or destroyed in the time intervals between the surveys.

If we consider the cycle of life in the sea, as represented in its simplest form in figure 248, we note that it is made up of two alternating phases, the inorganic and the organic, the latter being split into two parts by the plants and animals. Theoretically it should be possible to measure the amount of organic material produced by measuring the amount of material going through either the organic or inorganic portion of the cycle. Both methods are used, but both are beset with a number of difficulties, as will be noted below. Since the pioneering work of Hensen (1887), much progress has been made toward numerical values of the production of the sea, yet the best that can be claimed for these at present is that they are rough approximations only.

Phytoplankton Production

Data on phytoplankton production may be obtained by direct census or pigment analysis of the phytoplankton population, or through chemical analysis of the water in which it has grown.

Direct Census. Any sample of the population is only a measure of the *standing crop,* that is, the density of individuals or total volume or weight present at the moment and place of sampling. The common method of phytoplankton population analysis consists of centrifuging or filtering a known volume of water and counting directly under the microscope the number of cells of species making up the population thus concentrated. The population is then reported in numbers of cells of the various species prevailing per liter or per cubic meter of the water.

This method is essential to detailed analysis of the constituents of the phytoplankton communities and for arriving at an understanding of the factors operative in controlling the production of the different ecological types. To illustrate this it is necessary only to recall the plankton diatom types of Cleve (see p. 791) or to consider the divergence of requirements of the two main synthesizing groups, namely the diatoms and dinoflagellates. When the capacity of diatoms to continue a lively rate of organic production drops with increasing temperatures or diminution of essential nutrients, this drop is often in part compensated for by a flare of production by the warmth-loving dinoflagellates, which by reason of their low nutrient requirements and their motility may be able to utilize the nutrients below the lower threshold for spring diatoms (see p. 385).

It is, however, extremely difficult to arrive at accurate estimates of volumes or weights of organic matter through plankton counts alone, since diatom and dinoflagellate species and even individuals of the same species vary greatly in size and organic content and an appreciable portion of the diatoms is inorganic material forming the siliceous shells. Measurements of volume are sometimes made by centrifuging or allowing the plankton catch to settle in graduate cylinders and noting the volume of the precipitated material in milliliters. This method, however, does not serve to separate plant from animal material and the widely different types of organisms with respect to radiating spines and fluid content prevent comparable compactness in settling, with the result that the volume readings represent relative values which give only the major differences. This objection is partly overcome by measuring the total catches in terms of the number of milliliters of fluid which they displace. This is accomplished by noting the fluid volume before and after filtering out all of the organisms. It is not possible however, completely to drain off all of the water, hence the volume obtained includes the water residue and also the inorganic structures of the organisms.

PLANT PIGMENTS AND OTHER PLANKTON EQUIVALENTS. In view of the fact that the direct plankton measurements are inadequate for arriving at figures of total vegetative organic matter in the standing crop or the total production for a given period of time, attempts are made to use chemical analysis of the essential plant nutrients that have been consumed from the water by the plants in their production.

In order to estimate the organic content of a standing crop of phytoplankton, Harvey (1934) has described an adaptation of the method of Kreps and Verjbinskaya (1930) whereby the yellow-green pigment present in the plants filtered from a known volume of water is extracted by acetone and the pigment thus obtained in a known volume of acetone solution is determined colorimetrically with an arbitrary standard of 25 mg of potassium chromate and 430 mg of nickel sulphate dissolved in 1 l of water. One milliliter of the standard solution is equivalent to one "pigment unit" of chlorophyll. This pigment unit amounts to $0.88 \pm .01$ μg ($1\ \mu\text{g} = 0.001$ mg) of chlorophyll (Riley, 1938) or the equivalent of 3.3×10^{-3} mg of organic carbon. The total organic carbon content can then be calculated for the volume of water filtered. For more direct comparison with plankton counts it is also computed that, in the English Channel, one pigment unit is equal to 4000 diatoms of "average cell contents." Additional plankton equivalents are summarized in table 101, compiled by Fleming (1940).

In this table the "wet plankton" is defined by Atkins (1923) according to whom 1520 mg of wet plankton contains one milligram of phosphorus. This definition, however, is not based on analyses of phytoplankton but of seaweed and may be subject to revision. The equivalents of dry plankton, settling volumes, and displacement volumes are based on observations by Moberg and by M. W. Johnson (unpublished material). The equivalents of carbon, nitrogen, and phosphorus are based on the experimental results that the ratios $C:N:P = 41:7.2:1$ by weight. If other ratios are introduced, the equivalents must be altered correspondingly. The oxygen equivalent is obtained by assuming that the oxidation of one atom of carbon requires two atoms of oxygen, but Gilson (1937) suggests that the oxygen equivalent should be 20 per cent greater because allowance should be made for the oxygen consumed in oxidizing ammonia to nitrate.

So far, we have dealt with population only. To arrive at the total production of diatoms, for example, for a given unit of time it is necessary to have a series of samples over an interval of time so that calculations can be made on the basis of differences between the standing crops at each sampling. The average reproductive rate of diatoms constituting the population, the rate at which they are regularly eaten by the animal

TABLE 101

PLANKTON EQUIVALENTS

(Ratios, C:N:P = 41:7.2:1, by weight)

	Carbon (1 mg)	Nitrogen (1 mg)	Phosphorus (1 mg)	Plant pigment (1 unit)	Wet plankton (1 mg)	Dry plankton (1 mg)	Settling volume (1 ml)	Displacement volume (1 ml)	Oxygen equivalent (1 ml)
Carbon (mg)	1	5.7	41	3.3×10^{-3}	0.027	0.44	1.4	5.6	0.536
Nitrogen (mg)	0.18	1	7.2	0.58×10^{-3}	0.0047	0.0765	0.24	1.0	0.097
Phosphorus (mg)	0.024	0.14	1	0.08×10^{-3}	0.00066	0.011	0.034	0.14	0.013
Plant pigment (units)	305	1740	12,500	1	8.25	133	412	1690	163
Wet plankton (mg)	37	211	1,520	122×10^{-3}	1	16	50	203	20
Dry plankton (mg)	2.3	13.1	94	7.5×10^{-3}	0.06	1	3.1	12.7	1.2
Settling volume (ml)	0.7	4.2	30.2	2.4×10^{-3}	0.02	0.32	1	4.1	0.4
Displacement volume (ml)	0.18	1.0	7.4	0.59×10^{-3}	0.005	0.08	0.25	1	0.1
Oxygen equivalent (ml)	1.9	10.6	76	6.1×10^{-3}	0.05	0.8	2.5	10.2	1

plankton (cf. p. 901), and perhaps also the rate at which they sink below the euphotic zone are factors for which corrections must be made in the final calculations. An example from Lohmann's observations (1908) at Kiel will illustrate the procedure. Lohmann calculated that the daily plant increment was 30 per cent of the standing crop, that the protozoan animals consume daily one half their own weight in plants, and that the metazoan animals (copepods and other forms above the protozoa) consume daily one tenth their own weight. The daily phytoplankton *production* would then amount to the 30 per cent increase assigned to the rate of production, but if this increase be exactly the same as the day's ration required by the volume of animals present per cubic meter of water for the day, the standing crop of diatoms would show no increase for the day.

As stated elsewhere, Lohmann arrived at figures indicating a plant production of 10 mm^3/m^3 during February, the month of minimum plant production. But though the animals were few during the same period their food requirement was 18 mm^3/m^3. This left a daily deficiency of 8 mm^3/m^3 in food production for the month. The standing crop must therefore have been on a decline due to grazing, provided the animals at that season actually consumed the normal ration calculated for that month. On the other hand, most months showed a considerable surplus in production of plant material per cubic meter of water over that of consumption by animals. In August, the month of highest production, this surplus amounted to 290 mm^3/m^3. During that month the animals were also numerous and required a daily supply of food equal to 60 mm^3/m^3. Therefore the daily total organic material produced in August must have been 290 + 60, or 350 mm^3/m^3.

It should be noted here, however, that the production and consumption rates are not so simply estimated as assumed in these calculations. The rate of diatom division is not constant as here indicated, but may vary within wide limits between individuals or species, depending upon nutritional and physical factors which vary greatly over the year. Gran (1929) estimated that *Ceratium* spp. during the summer may have a daily increase of 30 per cent whereas some diatoms, for example *Chaetoceros curvisetum,* under favorable conditions may increase over 350 per cent daily. Thus during the period of maximum volumes of plants the conditions for rapid multiplication must have been more pronounced than during the periods represented by minimum volumes. With regard to consumption by animals, recent information indicates that the grazing animals apparently do not eat a fixed ration daily in relation to their weight, but instead during periods of high phytoplankton production eat much more than they can digest. This undoubtedly applies to filter feeders, which consume amounts of plants proportional to the concentration of the plants in suspension during the time of filtering. The rate of feeding is also controlled by such external factors as temperature. In view of the uncertainties involved in computation of production on the basis of observed changes in population, attention has been directed in recent years toward estimates of production on the basis of changes in the concentrations of essential plant nutrients or on the basis of observations as to oxygen production or consumption.

PLANT-NUTRIENT CONSUMPTION AS AN INDEX OF ORGANIC PRODUCTION. Changes in the concentrations of the essential plant nutrients coincident with plant growth are highly useful as indexes of production. Redfield, Cooper, and others have demonstrated the existence of a rather constant ratio between the elements carbon, nitrogen, and phosphorus in the organic content of mixed plankton (p. 768). The ratios C:N:P = 41:7.2:1 by weight, or 106:16:1 by atoms, are also in close agreement with the proportions of these elements in sea water (p. 236). Therefore a measurement of the drop in any one of these elements in the mineralized state in the sea water could reasonably be supposed to indicate an equivalent incorporation into organic material during synthesis of carbohydrates or proteins. The assimilation of CO_2 and its effect on *p*H was used as an index by Moore in estimating the organic production in the Irish Sea (p. 768) and it has subsequently been used elsewhere in conjunction with other chemical changes associated with plant growth. When CO_2 utilization is used as an index, the respiration of animals and the tendency for CO_2 of the water to be in equilibrium with that in the air must be taken into consideration.

During winter in the higher latitudes there is a maximum accumulation of *phosphate* in the water. This, when returned to the euphotic zone, is the available supply for the following spring growth of plants. In chapter XVI we noted that in some areas a vigorous consumption by plants may lead to a depletion of this nutrient during the growing season. In such an event the area has yielded its maximum production until further regeneration has taken place or further renewal has occurred, for instance by currents from subsurface nutrient-rich layers or by influx from elsewhere. There is considerable variation from year to year in the amount of phosphate that has been drawn upon by the plants and this must be a reflection of the variability in the capacity of plants to use the supply available because of other environmental factors either inorganic or organic which promote or retard the use of the nutrient. In a review of phosphate records covering fourteen years of observations in the English Channel, Cooper (1938) found that the percentage consumption of the total inorganic phosphate of the water column fluctuates between 49 per cent and 81 per cent for the spring productive period and between 63 per cent and 93 per cent for the entire period between the winter maximum and the summer minimum of phosphate. He points out that by April, on an average, one half of the phosphate supply for the year has been used up. An average annual utilization of about 78 per cent of the available supply, if occurring in such areas as the Antarctic or Puget Sound, where the store of phosphate is high, would lead to an exceedingly high annual organic production. Not only is there variability in the efficiency of plants in the utilization of phosphate, but the supply also varies from year to year owing to the nature of water flowing into the region. For example, Cooper's figures show that the average maximum phosphate supply available for the vernal plant production varies from an average of 0.67 μg-atom/L to only 0.47 μg-atom/L. This has a profound effect on both plant and animal production. Years of low phosphate are correlated with scarcity of plankton animals and poor production of young fish. The differences between the winter maximum and summer minimum of phosphate can, however, give only an approximate minimal measure since in the euphotic zone some regeneration of phosphate is known to occur, which would permit of interseasonal turnover in the supply and thus make possible a greater total production.

In connection with phosphate regeneration it should be pointed out here that when a higher concentration of phosphate occurs in isolated areas below the euphotic zone than occurs in the waters forming the regular source supply of phosphate to the euphotic layer, such phenomena must indicate that the excess phosphate has been regenerated *in situ.* The high phosphate values reflect a high organic production in the immediate overlying waters or in the surface layers of the region from which the phosphate-rich water spreads out. In these instances the growing organisms have served to entrap the phosphate in their bodies which subsequently sink and decay at intermediate depths, thus leading to high concentrations of this substance in these layers. As illustrative of this cycle, see fig. 45, p. 239. Such areas also show low oxygen content as a result of oxidation of organic material.

As a complementary study to phosphate utilization Harvey *et al* (1935) made analysis of the phosphorus compounds of the planktonic organisms. They found only a fraction of the phosphate removed from the water to be present in the plankton population, and concluded that much of the organic phosphorus compounds passes through the animals undigested and is then dissolved in the water until it is later regenerated to inorganic state.

The utilization of *nitrate* by the growing phytoplankton also gives an index of seasonal production. The various steps in the regeneration (see p. 913) are believed to retard the process so that nitrate accumulation during winter is especially pronounced in the northern latitudes, where well-defined growing seasons occur. However, since it is only the nitrogen that plants require from this compound, they can acquire this nitrogen from ammonia, and perhaps also from amino acids. Ammonia is an early product of putrefaction of organic material (p. 914), and therefore the nitrogen supply may, like that of the phosphate, experience some interseasonal turnover in its inorganic and organic phases.

OXYGEN PRODUCTION AND CONSUMPTION AS AN INDEX OF ORGANIC PRODUCTION. The plants obtain carbon for carbohydrate synthesis from the CO_2 in the water according to the equation

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2.$$

Above the level of the compensation depth (p. 779), so much oxygen is evolved as a by-product that the surrounding water may become supersaturated. A measure of this *oxygen production* provides a means of calculating the amount of carbon that has been bound in organic compounds. For each 1 ml of oxygen set free, 0.536 mg of carbon has been assimilated. Experiments on the rate of assimilation at various depths in the Gulf of Maine (table 93, p. 777) showed a maximum oxygen production of 2.33 ml/l at the surface in 9 hours and 10 minutes. The oxygen production decreased with depth and reached zero at a depth of about 44 m. For the whole water column beneath 1 m^2 the total production of oxygen equaled 29.1 l, corresponding to a fixation of 15.6 g of carbon for the duration of the experiment. This example illustrates part of the technique which can be employed in order to determine the gross production in the sea. In the quoted experiment the submerged water samples were all taken from the surface layers and the plankton associations in the bottles were therefore not identical with those at the depths where the bottles were exposed. In order to obtain correct values of the gross production in any locality, plankton samples should be taken from a series of depths and should be exposed at these depths, but so far no results of such experiments have been published.

In the experiment to which we have referred (table 93, p. 777), the exposed plankton association was a mixture of phyto- and zooplankton. The respiration of both plants and animals is therefore included, and this explains the high observed values of the respiration. Observations on pure cultures of phytoplankton organisms indicate that the ratio of respiration to maximum photosynthesis is usually less than 10 per cent. In a pure culture of *Nitzschia closterium* (Barker, 1935a) this ratio was 8 per cent; in a pure culture of a species of *Peridinium* (Barker, 1935b) it varied from 7 per cent to 14 per cent; in another culture of *Nitzschia closterium* (Clarke, 1936) it was less than 1 per cent; and in an apparently pure culture of *Coscinodiscus excentricus* (Jenkin, 1937) it varied from 3 per cent to 12 per cent.

In these instances the phytoplankton production would nearly equal the gross production, but the values were obtained under conditions when photosynthesis was rapid. On an average for a whole year the ratio of respiration to assimilation must be greater and may in some regions be as high as 50 per cent, in which case the phytoplankton production will be only half of the gross production (Riley, 1941).

The efficiency of the gross production, that is, the fraction of the energy penetrating the sea surface which is utilized in photosynthetic activity, is, in Long Island Sound, 0.55 to 0.82 per cent (Riley, 1941).

In nature, the oxygen accumulates in the layers of organic production and thus its fluctuations in time and space give a measure of the intensity of phytoplankton outbursts. It can provide only minimal values because the exact quantity of oxygen produced is obscured by the respiratory activities of animals and bacteria, and in case of surface supersaturation some oxygen is given off to the atmosphere.

Associated with the above is the problem of estimating the production of organic material by a study of the oxygen *consumed* in the eventual oxidation of the material below the water layers in which it was produced. This association necessitates a consideration of the oxygen used in the oxidation of the carbon and in converting ammonia to nitrates, but the hydrography of the area must be such that the water layer in which oxygen consumption is being measured can be definitely referred to the euphotic layer in which the production of organic material is supposed to have occurred some time previously. As yet no method has been developed by which the amount of oxygen consumed can be determined directly, but indirectly it can be found if it is assumed that in the subsurface layer the distribution of oxygen is stationary (p. 161). On this assumption the amount of oxygen which in unit time is brought into a given volume by processes of diffusion and advection must equal the amount which in the same time is consumed in the same volume. The replenishment of oxygen by diffusion and advection can be determined if sufficient hydrographic data are available (for example, Seiwell, 1935, Sverdrup and Fleming, 1941), and so far our knowledge of oxygen consumption in the subsurface layers is derived from such computations only.

In closing this brief review of the various indices of organic production in the sea, it may be stated that the most reliable figures are, doubtless, to be obtained by a combination of the various methods, both biological and chemical, in order to provide corroborative evidence.

Zooplankton Production

An approach to the problems of organic production of the sea is possible through a study of zooplankton production, since the animals of this group are in general the chief grazers and must fluctuate with the supply of their food (cf. p. 899). They are vastly more numerous and regularly distributed than the predatory animals and any fluctuations in population numbers are not influenced by fishing.

That the production of zooplankton is indeed large may be seen from Redfield's analysis (1941) of the standing calanoid population of the Gulf of Maine. The average monthly catch for all sections of the Gulf was about 40 ml of water-free plankton per square meter of surface. The highest monthly value, 90 ml, was obtained in September and the lowest value, about 10 ml, was obtained in May. Water-free or dry plankton volumes were obtained by filtering the water from the animals. This allows them to become more compact than when measuring the volume by precipitation in fluid. The latter method gave volumes usually about 4.9 times greater.

On the basis of the above water-free values the standing crop for the whole Gulf would be some four million tons. The crop increased by about 80 ml of water-free plankton per square meter between May and September, which is a net gain of about eight million tons. In the English Channel the *maximum* standing crop for zooplankton in 1934 was calculated (Harvey *et al*, 1935) at about 40 mm^3 per 100 liters. Considering the depth at 100 m, this would be about 40 ml/m^2 of surface, or the average annual value found for the Gulf of Maine. If the zooplankton production is to be considered a measure of the phytoplankton production, many factors tending to vary the volume of zooplankton in relation to the plants have to be taken into account. We enumerate the four following:

(1) Much of the zooplankton is consumed by predatory plankton feeders that live regularly in the area of production or that enter it as invaders from less productive areas. The extent of such consumption is not known, but we know, for instance, that rich herring hauls are correlated with abundant *Calanus,* and that plankton-feeding whales also seek out productive waters such as those of the Antarctic and of northern coastal banks that are rich in their favorite food (p. 905). It has been estimated that on an area 8,000,000 km^2 there may be as many as 300,000 whales. The food required by these animals alone must be enormous. They may grow to a length of nearly 28 m and a weight of 80 tons in about two years. Their resting metabolism requires 38 l of oxygen per minute (p. 907). The energy required for this rapid growth and katabolic processes must make notable inroads on the animal plankton.

(2) Many of the plankton animals eat more plants than they can use in their metabolic processes and thus pass through the digestive tract much undigested material during periods of high plant production. This waste makes it impossible to assign a fixed value to the amount of food that animals of a given weight should consume per day to grow and repair breaking-down processes within certain temperature ranges. If a figure for consumption is to be obtained for filter-feeding forms it would

be necessary to determine the average rate at which phytoplankton of different densities is screened from the water (cf. p. 902).

(3) Few plankton animals are strictly plant eaters, but instead have a mixed diet of plants and animals or of detritus arising from both, while yet others are wholly carnivorous. The direct relationship of the zooplankton production to the phytoplankton as a source of energy is in this way obscured and separated in time.

(4) Finally, much of the phytoplankton production is not consumed by planktonic animals but instead sinks to the bottom to serve as food for benthic animals or dies and becomes food directly for the bacteria without the intervention of animals at all.

Commercial Production

Studies may be concerned primarily with the amount of organic material represented in tons per year of fish over certain fishing grounds, the poundage yield of oysters on cultivated beds, or the season's yield in barrels of oil from whales. These are evaluations of commercially important yields and though they do have a direct relation to the total organic production in certain sections of the sea, yet they are too far removed from the original source of synthesis of organic material to give anything more than a very general picture of production of the sea; for we do not know the ratio between the volume of fish, and so forth, and the volume of plants which, through various animal transformations, have supplied the food for growth and other vital energy-consuming processes of these and the intermediary animals. The yield of commercially sought animals is also subject to change through the influence of man and may therefore not give a true value representing their place in the balance of nature. Nevertheless, in semiclosed areas it is possible to arrive at figures which illustrate in a broad way the relationship in production of plants and herbivorous and carnivorous animals. Petersen (1918) has made certain calculations of the quantitative food relations of important animals in coastal waters where eelgrass, *Zostera*, furnishes the main source of primary food. This relationship is diagrammatically shown in fig. 249, from his report. As a working hypothesis he has assumed that each unit of weight of herbivorous animal substance requires ten units of plant substance in its formation, and each unit of weight of carnivorous organism feeding directly upon herbivorous forms requires ten units of the latter, hence one hundred plant units are needed to produce each unit of a carnivorous animal such as is represented by the plaice, for instance. But many carnivorous forms such as the cod feed only upon carnivorous animals, as shown by the radiating arrows in the figure, and this habit entails another similar loss as the length of the chain of transformers is increased, with the result that it has required a thousand units weight of *Zostera* to produce one unit weight of cod or similar animal. The "useless" animals are supposed to be those not eaten by animals constituting fish food, and they form a plant-animal cycle of their own.

From these calculations, which can give only rough approximations, we can at least obtain some perception of the vast quantity of plant substance involved in production of a small amount of carnivorous animal tissue, and in the light of this the world's production of fish, which is in the neighborhood of 13 million tons annually, takes on a new significance. Failure in production in the initial link of the food chain must be recorded in the series of sequences leading up to the predators of highest rank.

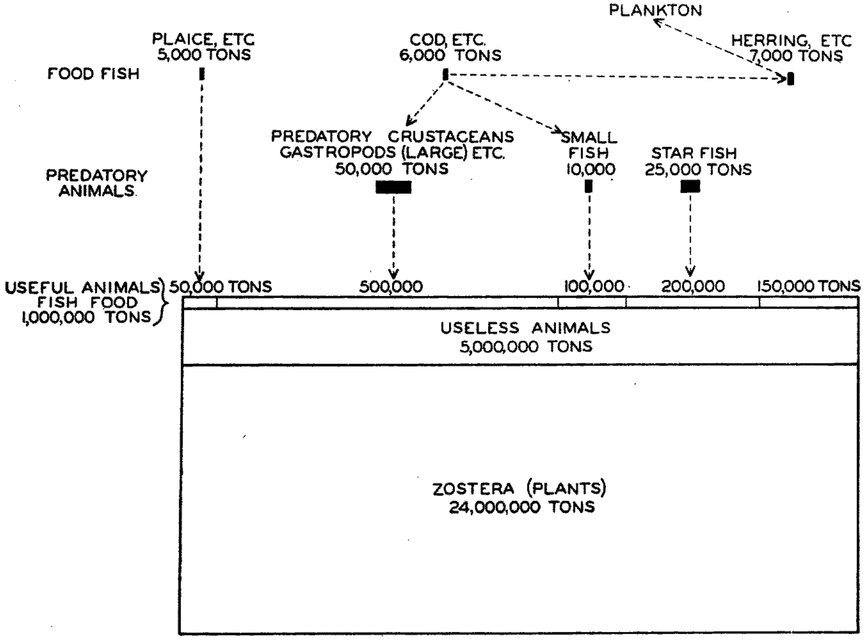

Fig. 249. Quantitative food relations of certain animals dependent on *Zostera* for the primary food. (After Petersen.)

The Production in Different Regions

It is very well known that some regions of the oceans give evidence of being on the whole more productive than others. Locally also, considerable variation exists in different coastal areas. We have already learned what some of the underlying reasons may be. Precise quantitative data on initial organic production are scanty and diverse as far as the methods of estimating and the period of time involved are concerned. In table 102, which is taken mainly from Riley (1941), some estimates are given from separate areas which will serve to illustrate the best available

Table 102
PRODUCTION
(After Riley, 1941)

	Location	Production Carbon (g/m²/yr)	Method	Authority
Experimental observations	Long Island Sound	600–1000	Gross production—O_2 production in experimental bottles	Riley, 1938, 1939, present paper
	Western Atlantic, 23°–38°N	530		
	Western Atlantic, 38°–41°N	320		
	Dry Tortugas	60–430		
	Long Island Sound	400–700	Phytoplankton production—O_2 production	
		440–875	P consumption	
		100–200	N consumption	
		95–190	Chlorophyll production	
	Western Atlantic, 23°–41°N	140–365	N consumption	
	Dry Tortugas	27	P consumption	
		5	Plant pigment production	
Observations on natural environment	Western Atlantic 3°–13°N	278	Oxygen consumption	Seiwell, 1935
	Off southern California	215–430		Sverdrup and Fleming, 1941
	Long Island Sound	384	Increase in oxygen—experimental	Riley
	English Channel	84	P consumption	Atkins, 1923
		98	Changes in CO_2	
		60	Changes in O_2	
		70	Changes in P	
		88	Changes in N	Cooper, 1938
		7	Changes in Si	
		5	Changes in Ca	
	Barents Sea	170–330	P consumption	Kreps and Verjbinskaya, 1930
	Long Island Sound	138–350	P consumption	Riley
Short-period experimental observations		Carbon (g/m³/day)		
	Norwegian coast	0.14		Gran, 1927
	Scottish coast	0.16		Marshall and Orr, 1930
	Dry Tortugas	0.07		
	Western Atlantic, 23°–41°N	0.01–0.12	Gross production—O_2 production in experimental bottles at the surface	Riley
	Western Atlantic—George's Bank	0–0.88		
	Long Island Sound	0.02–0.41		
	Scripps Institution pier	0.01–0.15		Sargent, manuscript

figures, in terms of grams of carbon per square meter or per cubic meter, on the order of magnitude of phytoplankton production.

Large seasonal variations in the nutrient elements have been observed in coastal areas in temperate latitudes where there are marked variations in the physical, chemical, and biological factors during the year. In the English Channel, which is only about 100 m deep, conditions are such that complete mixing from the surface to the bottom takes place in the winter months. Even during the summer this condition prevails for short periods, consequently the entire water column may be depleted of nutrients. In the Gulf of Maine a similar mixing occurs during the winter months and near Friday Harbor strong tidal currents and irregular topography contribute to intense vertical mixing throughout the year.

For these and other reasons (such as the proximity to land) the annual variations in the plankton population and in the distribution of the nutrient elements characteristic of these individual localities can not be applied to other regions or to the open sea without a careful consideration of the different factors which may be involved. In areas such as the English Channel, where the nutrients are more or less completely removed from the water column during the summer, it is quite probable that the amount of production is related to the store of nutrient elements present at the beginning of the vegetative season. In localities where there are vertical gradients in the nutrient concentrations, diffusion and turbulence will carry a certain amount into the euphotic zone. Such processes are so effective in certain areas, for instance near Friday Harbor, that plant development does not deplete the nutrients to a point where the amounts present can affect the rate of growth. In these areas other factors must limit the organic production (p. 769). In table 103 are given, for a number of localities, the approximate averages for the contents of nitrate, phosphate and silicate in the upper 25 m at the times

TABLE 103

WINTER MAXIMA AND SUMMER MINIMA IN NUTRIENT SALTS

(Average for 0–25 meters. Units: μg-atoms/liter.)

Locality	Latitude	NO_3-N		PO_4-P		SiO_3-Si	
		Max.	Min.	Max.	Min.	Max.	Min.
English Channel	50°N	7.	0	0.55	0	4.	0
Friday Harbor*	48°N	25.	15.	2.	1.	57.	42.
Gulf of Maine	43°N	12.	2.	1.	0.2		
South Georgia	54°S			1.7	0.9	30.	5.
Barents Sea	73°N	12.5	1.	0.63	0		

* Surface values only.

of the winter maxima and the summer minima. As shown previously, virtual depletion of the surface layers takes place in the English Channel and similar conditions occur in the Barents Sea, whereas at Friday Harbor (surface values only), in the Gulf of Maine and particularly around South Georgia, nutrient elements are present in the surface layers at all times.

In order to estimate the rate of production in areas where there is no marked seasonal change in the distribution of nutrients, it is necessary to take into account the supply of these materials which will result from diffusion. Even in localities where there is a marked seasonal change, estimates of production based on the removal of nutrients during the vegetative season must be corrected for this process or a layer of sufficient thickness to eliminate this factor must be used when calculating the total amount of any element removed from the water column. The latter method has been used at a number of localities to estimate the differences in the amounts of the nutrient elements in the water column at the times of winter maxima and summer minima. From these data, the net utilization in grams per square meter column of NO_3-N, PO_4-P and SiO_3-Si during the vegetative season have been obtained. The values are given in table 104. The net removal of nitrate and phosphate in the Barents Sea and around South Georgia is about twice as great as the utilization in the English Channel and in the Gulf of Maine. The great difference between the silicate utilization in the English Channel and around South Georgia is of interest in connection with the deposition of siliceous sediments. Estimates of seasonal production based on data of this kind are minimal because they include no consideration of the effects of regeneration, that is, that the elements may pass through the biological cycle more than once during the season. Kreps and Verjbinskaya (1932) estimate that, in the Barents Sea, production, calculated from the phosphate utilization, should be increased by about one third to correct for the concurrent regeneration.

TABLE 104

DIFFERENCE BETWEEN WINTER MAXIMUM AND SUMMER MINIMUM FOR THE WATER COLUMN

(Units: grams of elements per square meter of surface.)

Locality	Length of water column (m)	NO_3-N	PO_4-P	SiO_3-Si
English Channel	75	6.6	1.1	7.4
Gulf of Maine	100	7.0	1.2	
South Georgia	100		1.9	70.0
Barents Sea	200	11.0	1.9	

Many observations indicate a higher rate of organic production in the high latitudes than in the tropics. This possibility is brought out clearly in fig. 250, from the *Meteor* observations, where the standing population in the Antarctic is about tenfold that in the tropical regions. The greater standing crop in high latitudes may not indicate a greater annual production because in high latitudes the production is concentrated into a few months of vigorous and spectacular growth with return of sunshine or following nutrient replenishment over the winter, whereas in the lower latitudes the growth may proceed at a slower but more continuous rate as nutrients become available.

The marked cycle of meteorological events characteristic of temperate and high latitudes leads to a number of associated phenomena vital in determining the periodicity and extent of organic production in these latitudes. The decrease of sunlight inhibits or diminishes growth during the darkest winter months and the low winter surface temperatures give rise to active convection currents effecting an abundant annual renewal of essential plant nutrients in the euphotic layer. In the Gulf of Maine these currents reach a depth of 100 m, and in shallower areas the whole column of water with its store of nutrients is involved in the mixing. Spring and summer conditions bring about a stabilization which, together with an ample supply of solar energy, provides the conditions essential for a vigorous though short period of production. Reference to the discussion of hydrographic conditions in the Antarctic will show that in that region the ascent of deep water near the Antarctic Continent brings to the surface waters an excessively rich supply of nutrients which, in moving toward the Antarctic Convergence (fig. 164, p. 620), give rise to a great flare of diatom production during the Antarctic spring and summer when sunshine is ample and the upper water layers have become stabilized through melting of northward-drifting ice (Hart, 1934). So great is the

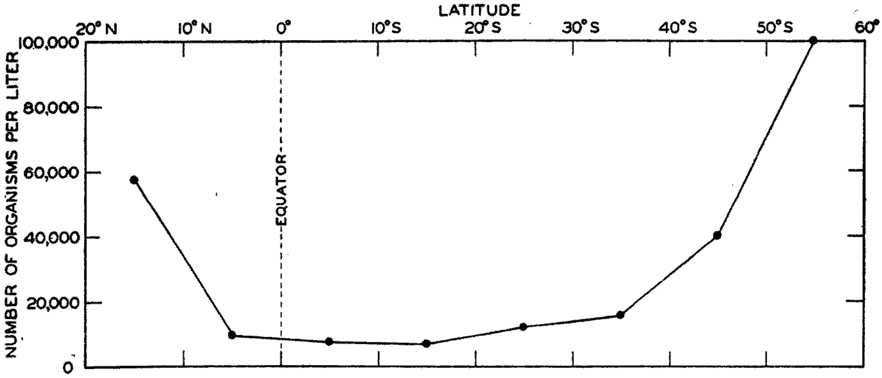

Fig. 250. The quantity of total plankton organisms in the upper 50 m of high- and low-latitude waters of the South Atlantic.

supply of nutrients in the euphotic zone that depletion of these salts never becomes a limiting factor, since the content never falls below a minimum of about 0.9 μ-atom of PO_4 per liter. This leaves a summer minimum higher than the winter maximum of the English Channel. In the Antarctic the checks on production are not clearly understood, but they are perhaps associated with conditions of light and stability of the surface layers. The excessively dense masses which discolor the water (figs. 214 and 216, pp. 784 and 786) must produce a screening of light that leads to regulation of photosynthesis. The large volumes of zooplankton occurring in this region must indicate that grazing is also an important factor in control.

That plankton production is indeed great in the Antarctic in spite of the short season is proven by the invasion of large numbers of feeding whales which migrate each year to these waters to fatten on the rich supply of available food there. The bottom fauna of these areas is also unusually rich, as was found by the *Challenger* and other expeditions. That diatom production is perhaps even greater than its animal utilization during the maximum growing period is suggested by the accumulation of the broad band of diatomaceous ooze so characteristic of the bottom deposits encircling the Antarctic Continent (fig. 253, p. 975). Hart has pointed out, however, that the types of diatoms found in these oozes belong largely to species which go unaltered through the digestive tracts of animals.

As to production in lower latitudes we can say that in general the open sea is relatively sterile (figs. 214 and 216, pp. 784 and 786). Examinations of figs. 217 and 218, pp. 787 and 788, will show why this must be so, for the supply of nutrients lies below the euphotic zone and the strong and persistent thermal stratification of the water within this zone precludes any complete or rapid renewal of nutrients in the upper layers despite the greater thickness of the euphotic layer in tropical or subtropical regions. In coastal areas with upwelling or in offshore regions of divergence, the situation is quite different. As an example of the former we have already mentioned the west African coast (p. 786). We may consider also the Peru Current, which in the tropical and subtropical regions brings to the surface an abundant continuous supply of nutrients that provide fertilization for heavy phytoplankton production, near the coast mainly but also in some sections in almost undiminished intensity to a distance of 320 km seaward (Gunther, 1936). The great production of this oceanic system is manifest in the tremendous quantities of marine birds in this area. Some idea of the magnitude of production can be had from Schott's report (1932) that on one small island of the Chinchas group there are estimated to be some five or six million marine birds, such as cormorants, pelicans, and gannets, which daily remove at least 1000 tons of small fish from the surrounding water. The great Peruvian guano deposits on the shores of these regions may be as much as 30 m in thickness.

In comparing the great productivity of the Peru Current with that of the Antarctic, it must be borne in mind that the latter system is one of very great geographic extent while the former, like other highly productive areas in lower latitudes, is more localized and to that degree of less general significance in the economy of the region as a whole. The greater fisheries of the north and north temperate regions are in themselves indicative of great organic production and they have profoundly influenced the settlement of coastal areas by man.

It should be mentioned that the question of relative production in high and low latitudes is still an open question. Some evidence points to a greater production in the latter than has been indicated by the various oceanographic expeditions whose data have been concerned mainly with the open sea. An example of subtropical production in a restricted area is offered by the investigations of the Great Barrier Reef Expedition.

In using the zooplankton as an index of productivity, Russell (1934) concluded that the Great Barrier Reef lagoon was somewhat richer in numbers of plankton animals than all but one of five representative stations in the North Sea and the English Channel. Over two years the monthly average at these northern stations was 2815 animals per vertical haul with a 50-cm net, while a one-year investigation with a similar net, used in the same fashion in the Barrier Reef lagoon, showed the number of animals to be 5684 per haul. Usually copepods made up 70 per cent or more of the animals. In tropical regions copepods are usually less than 1 mm in length, while in the north the most abundant species are over 1.5 mm in length. When allowance is made for this small size and for a supposedly more rapid rate of metabolism for the tropical species, the conclusion is that the two areas are about equal in production of zooplankton. The phytoplankton was always scanty in the Barrier Reef lagoon, however, and this appears to be of special interest in indicating that the area was supporting its maximal zooplankton population and that, because of the even rate of phytoplankton production, no surplus of plants was being produced as it is in higher latitudes during the height of the growing season. This equilibrium is of significance also in the study of sedimentation, for it is in the high latitudes that the diatom oozes are found.

Recent studies indicate a need to consider more closely the significance of the vastly deeper euphotic zone of the tropical seas. In one investigation (Riley, 1939) it was found, for example, that in stations of latitude about 40°N plant pigments were most abundant at the surface, the maximum depth of occurrence being 100 m, whereas at tropical and subtropical stations the pigments were most abundant at 100 m and at depths of 300 to 400 m.

Many investigations have indicated a lower production of phytoplankton and zooplankton in the oceanic waters than in the neritic waters. The blueness of the waters of the open sea, as indicated in fig. 214, p. 784, is correlated with this fact. This difference is what one would expect, since the ease of nutrient renewal both by water circulation and by runoff from land is all in favor of the coastal regions. The offshore regions are favored, however, by a greater transparency of the water owing to the absence of suspended particles of terrigenous origin.

In neritic areas, the diatoms form resting spores that are believed to be important in quickly "seeding" the waters when favorable conditions return. The oceanic flora depends upon survival of sporeless individuals to initiate the crop. This may at times result in a scarcity of suitable species to take advantage of the return of favorable conditions (see p. 770), but a limited nutrient supply is doubtless the main reason for low oceanic production.

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