vice versa. Perhaps, all this is evident, obvious, trite, a collection of truisms. If so, the obvious should be accepted and appropriate new programs planned.

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Photosynthesis and Fish Production in the Sea

The production of organic matter and its conversion to higher forms of life vary throughout the world ocean.

John H. Ryther

Numerous attempts have been made to estimate the production in the sea of fish and other organisms of existing or potential food value to man (*1–4*). These exercises, for the most part, are based on estimates of primary (photosynthetic) organic production rates in the ocean (*5*) and various assumed trophic-dynamic relationships between the photosynthetic producers and the organisms of interest to man. Included in the latter are the number of steps or links in the food chains and the efficiency of conversion of organic matter from each trophic level or link in the food chain to the next. Different estimates result from different choices in the number of trophic levels and in the efficiencies, as illustrated in Table 1 (*2*).

Implicit in the above approach is the concept of the ocean as a single ecosystem in which the same food chains involving the same number of links and efficiencies apply throughout. However, the rate of primary production is known to be highly variable, differing by at least two full orders of magnitude from the richest to the most impoverished regions. This in itself would be expected to result in a highly irregular pattern of food production. In addition, the ecological conditions which determine the trophic dynamics of marine food chains also vary widely and in direct relationship to the absolute level of primary organic production. As is shown below, the two sets of variables—primary production and the associated food chain dynamics—may act additively to produce differences in fish production which are far more pronounced and dramatic than the observed variability of the individual causative factors.

Primary Productivity

Our knowledge of the primary organic productivity of the ocean began with the development of the C^{14}-tracer technique for *in situ* measurement of photosynthesis by marine plankton algae (*6*) and the application of the method on the 1950–52 *Galathea* expedition around the world (*5*). Despite obvious deficiencies in the coverage of the ocean by *Galathea* (the expedition made 194 observations, or an average of about one every 2 million square kilometers, most of which were made in the tropics or semitropics), our concept of the total productivity of the world ocean has changed little in the intervening years.

While there have been no more expeditions comparable to the *Galathea*, there have been numerous local or regional studies of productivity in many parts of the world. Most of these have been brought together by a group of Soviet scientists to provide up-to-date world coverage consisting of over 7000 productivity observations (*7*). The result has been modification of the estimate of primary production in the world ocean from 1.2 to 1.5×10^{10} tons of carbon fixed per year (*5*) to a new figure, 1.5 to 1.8×10^{10} tons.

Attempts have also been made by Steemann Nielsen and Jensen (*5*), Ryther (*8*), and Koblentz-Mishke *et al.* (*7*) to assign specific levels or ranges of productivity to different parts of the ocean. Although the approach was somewhat different in each case, in general the agreement between the three was good and, with appropriate condensation and combination, permit the following conclusions.

1) Annual primary production in the open sea varies, for the most part, between 25 and 75 grams of carbon fixed per square meter and averages about 50 grams of carbon per square meter per year. This is true for roughly 90 percent of the ocean, an area of 326×10^6 square kilometers.

2) Higher levels of primary production occur in shallow coastal waters, defined here as the area within the 100-fathom (180-meter) depth contour. The mean value for this region may be considered to be 100 grams of carbon fixed per square meter per year, and the area, according to Menard and Smith (*9*), is 7.5 percent of the total world ocean. In addition, certain offshore waters are influenced by divergences, fronts, and other hydrographic features which bring nutrient-rich subsurface water into the euphotic zone. The equatorial divergences are examples of such regions. The productivity of these offshore areas is comparable to that of the coastal zone. Their total area is difficult to assess, but is considered here to be 2.5 percent of the total ocean. Thus, the coastal zone and the offshore regions of comparably high productivity together represent 10 percent of the total area of the

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oceans, or 36 × 10^6 square kilometers.

3) In a few restricted areas of the world, particularly along the west coasts of continents at subtropical latitudes where there are prevailing offshore winds and strong eastern boundary currents, surface waters are diverted offshore and are replaced by nutrient-rich deeper water. Such areas of coastal upwelling are biologically the richest parts of the ocean. They exist off Peru, California, northwest and southwest Africa, Somalia, and the Arabian coast, and in other more localized situations. Extensive coastal upwelling also is known to occur in various places around the continent of Antarctica, although its exact location and extent have not been well documented. During periods of active upwelling, primary production normally exceeds 1.0 and may exceed 10.0 grams of carbon per square meter per day. Some of the high values which have been reported from these locations are 3.9 grams for the southwest coast of Africa (*5*), 6.4 for the Arabian Sea (*10*), and 11.2 off Peru (*11*). However, the upwelling of subsurface water does not persist throughout the year in many of these places—for example, in the Arabian Sea, where the process is seasonal and related to the monsoon winds. In the Antarctic, high production is limited by solar radiation during half the year. For all these areas of coastal upwelling throughout the year, it is probably safe, if somewhat conservative, to assign an annual value of 300 grams of carbon per square meter. Their total area in the world is again difficult to assess. On the assumption that their total cumulative area is no greater than 10 times the well-documented upwelling area off Peru, this would amount to some 3.6 × 10^5 square kilometers, or 0.1 percent of the world ocean. These conclusions are summarized in Table 2.

Food Chains

Let us next examine the three provinces of the ocean which have been designated according to their differing levels of primary productivity from the standpoint of other possible major differences. These will include, in particular, differences which relate to the food chains and to trophic efficiencies involved in the transfer of organic matter from the photosynthetic organisms to fish and invertebrate species large and abundant enough to be of importance to man.

The first factor to be considered in this context is the size of the photosynthetic or producer organisms. It is generally agreed that, as one moves from coastal to offshore oceanic waters, the character of these organisms changes from large "microplankton" (100 microns or more in diameter) to the much smaller "nannoplankton" cells 5 to 25 microns in their largest dimensions (*12, 13*).

Since the size of an organism is an essential criterion of its potential usefulness to man, we have the following relationship: the larger the plant cells at the beginning of the food chain, the fewer the trophic levels that are required to convert the organic matter to a useful form. The oceanic nannoplankton cannot be effectively filtered from the water by most of the common zooplankton crustacea. For example, the euphausid *Euphausia pacifica*, which may function as a herbivore in the rich subarctic coastal waters of the Pacific, must turn to a carnivorous habit in the offshore waters where the phytoplankton become too small to be captured (*13*).

Intermediate between the nannoplankton and the carnivorous zooplankton are a group of herbivores, the microzooplankton, whose ecological significance is a subject of considerable current interest (*14, 15*). Representatives of this group include protozoans such as Radiolaria, Foraminifera, and Tintinnidae, and larval nuplii of microcrustaceans. These organisms, which may occur in concentrations of tens of thousands per cubic meter, are the primary herbivores of the open sea.

Feeding upon these tiny animals is a great host of carnivorous zooplankton, many of which have long been thought of as herbivores. Only by careful study of the mouthparts and feeding habits were Anraku and Omori (*16*) able to show that many common copepods are facultative if not obligate carnivores. Some of these predatory copepods may be no more than a millimeter or two in length.

Again, it is in the offshore environment that these small carnivorous zooplankton predominate. Grice and Hart (*17*) showed that the percentage of carnivorous species in the zooplankton increased from 16 to 39 percent in a transect from the coastal waters of the northeastern United States to the Sargasso Sea. Of very considerable importance in this group are the Chaetognatha. In terms of biomass, this group of animals, predominantly carnivorous, represents, on the average, 30 percent of the weight of copepods in the open sea (*17*). With such a distribution, it is clear that virtually all the copepods, many of which are themselves carnivores, must be preyed upon by chaetognaths.

Table 1. Estimates of potential yields (per year) at various trophic levels, in metric tons. [After Schaeffer (*2*)]

Trophic level	Ecological efficiency factor					
	10 percent		15 percent		20 percent	
	Carbon (tons)	Total weight (tons)	Carbon (tons)	Total weight (tons)	Carbon (tons)	Total weight (tons)
0. Phytoplankton (net particulate production)	1.9 × 10^{10}		1.9 × 10^{10}		1.9 × 10^{10}	
1. Herbivores	1.9 × 10^9	1.9 × 10^{10}	2.8 × 10^9	2.8 × 10^{10}	3.8 × 10^9	3.8 × 10^{10}
2. 1st stage carnivores	1.9 × 10^8	1.9 × 10^9	4.2 × 10^8	4.2 × 10^9	7.6 × 10^8	7.6 × 10^9
3. 2nd stage carnivores	1.9 × 10^7	1.9 × 10^8	6.4 × 10^7	6.4 × 10^8	15.2 × 10^7	15.2 × 10^8
4. 3rd stage carnivores	1.9 × 10^6	1.9 × 10^7	9.6 × 10^6	9.6 × 10^7	30.4 × 10^6	30.4 × 10^7

Table 2. Division of the ocean into provinces according to their level of primary organic production.

Province	Percentage of ocean	Area (km^2)	Mean productivity (grams of carbon/m^2/yr)	Total productivity (10^9 tons of carbon/yr)
Open ocean	90	326 × 10^6	50	16.3
Coastal zone*	9.9	36 × 10^6	100	3.6
Upwelling areas	0.1	3.6 × 10^5	300	0.1
Total				20.0

* Includes offshore areas of high productivity.

Table 3. Estimated fish production in the three ocean provinces defined in Table 2.

Province	Primary production [tons (organic carbon)]	Trophic levels	Efficiency (%)	Fish production [tons (fresh wt.)]
Oceanic	16.3×10^9	5	10	16×10^5
Coastal	3.6×10^9	3	15	12×10^7
Upwelling	0.1×10^9	1½	20	12×10^7
Total				24×10^7

The oceanic food chain thus far described involves three to four trophic levels from the photosynthetic nannoplankton to animals no more than 1 to 2 centimeters long. How many additional steps may be required to produce organisms of conceivable use to man is difficult to say, largely because there are so few known oceanic species large enough and (through schooling habits) abundant enough to fit this category. Familiar species such as the tunas, dolphins, and squid are all top carnivores which feed on fishes or invertebrates at least one, and probably two, trophic levels beyond such zooplankton as the chaetognaths. A food chain consisting of five trophic levels between photosynthetic organisms and man would therefore seem reasonable for the oceanic province.

As for the coastal zone, it has already been pointed out that the phytoplankton are quite commonly large enough to be filtered and consumed directly by the common crustacean zooplankton such as copepods and euphausids. However, the presence, in coastal waters, of protozoans and other microzooplankton in larger numbers and of greater biomass than those found in offshore waters (*15*) attests to the fact that much of the primary production here, too, passes through several steps of a microscopic food chain before reaching the macrozooplankton.

The larger animals of the coastal province (that is, those directly useful to man) are certainly the most diverse with respect to feeding type. Some (mollusks and some fishes) are herbivores. Many others, including most of the pelagic clupeoid fishes, feed on zooplankton. Another large group, the demersal fishes, feed on bottom fauna which may be anywhere from one to several steps removed from the phytoplankton.

If the herbivorous clupeoid fishes are excluded (since these occur predominantly in the upwelling provinces and are therefore considered separately), it is probably safe to assume that the average food organism from coastal waters represents the end of at least a three-step food chain between phytoplankton and man.

It is in the upwelling areas of the world that food chains are the shortest, or—to put it another way—that the organisms are large enough to be directly utilizable by man from trophic levels very near the primary producers. This, again, is due to the large size of the phytoplankton, but it is due also to the fact that many of these species are colonial in habit, forming large gelatinous masses or long filaments. The eight most abundant species of phytoplankton in the upwelling region off Peru, in the spring of 1966, were *Chaetoceros socialis*, *C. debilis*, *C. lorenzianus*, *Skeletonema costatum*, *Nitzschia seriata*, *N. delicatissima*, *Schroederella delicatula*, and *Asterionella japonica* (*11*, *18*). The first in this list, *C. socialis*, forms large gelatinous masses. The others all form long filamentous chains. *Thalossiosira subtilis*, another gelatinous colonial form like *Chaetoceros socialis*, occurs commonly off southwest Africa (*19*) and close to shore off the Azores (*20*). Hart (*21*) makes special mention of the colonial habit of all the most abundant species of phytoplankton in the Antarctic—*Fragiloriopsis antarctica*, *Encampia balaustrium*, *Rhizosalenia alata*, *R. antarctica*, *R. chunii*, *Thallosiothrix antarctica*, and *Phaeocystis brucei*.

Many of the above-mentioned species of phytoplankton form colonies several millimeters and, in some cases, several centimeters in diameter. Such aggregates of plant material can be readily eaten by large fishes without special feeding adaptation. In addition, however, many of the clupeoid fishes (sardines, anchovies, pilchards, menhaden, and so on) that are found most abundantly in upwelling areas and that make up the largest single component of the world's commercial fish landings, do have specially modified gill rakers for removing the larger species of phytoplankton from the water.

There seems little doubt that many of the fishes indigenous to upwelling regions are direct herbivores for at least most of their lives. There is some evidence that juveniles of the Peruvian anchovy (*Engraulis ringens*) may feed on zooplankton, but the adult is predominantly if not exclusively a herbivore (*22*). Small gobies (*Gobius bibarbatus*) found at mid-water in the coastal waters off southwest Africa had their stomachs filled with a large, chain-forming diatom of the genus *Fragilaria* (*23*). There is considerable interest at present in the possible commercial utilization of the large Antarctic krill, *Euphausia superba*, which feeds primarily on the colonial diatom *Fragilariopsis antarctica* (*24*).

In some of the upwelling regions of the world, such as the Arabian Sea, the species of fish are not well known, so it is not surprising that knowledge of their feeding habits and food chains is fragmentary. From what is known, however, the evidence would appear to be overwhelming that a one- or two-step food chain between phytoplankton and man is the rule. As a working compromise, let us assign the upwelling province a 1½-step food chain.

Efficiency

The growth (that is, the net organic production) of an organism is a function of the food assimilated less metabolic losses or respiration. This efficiency of growth or food utilization (the ratio of growth to assimilation) has been found, by a large number of investigators and with a great variety of organisms, to be about 30 percent in young, actively growing animals. The efficiency decreases as animals approach their full growth, and reaches zero in fully mature or senescent individuals (*25*). Thus a figure of 30 percent can be considered a biological potential which may be approached in nature, although the growth efficiency of a population of animals of mixed ages under steady-state conditions must be lower.

Since there must obviously be a "maintenance ration" which is just sufficient to accommodate an organism's basal metabolic requirement (*26*), it must also be true that growth efficiency is a function of the absolute rate of assimilation. The effects of this factor will be most pronounced at low feeding rates, near the "maintenance ration," and will tend to become negligible at high feeding rates. Food conversion (that is, growth efficiency) will therefore obviously be related to food availability, or to the concentration of prey organisms when the latter are sparsely distributed.

In addition, the more available the food and the greater the quantity consumed, the greater the amount of "internal work" the animal must perform to digest, assimilate, convert, and store the food. Conversely, the less available the food, the greater the amount of "external work" the animal must perform to hunt, locate, and capture its prey. These concepts are discussed in some detail by Ivlev (*27*) and reviewed by Ricker (*28*). The two metabolic costs thus work in opposite ways with respect to food availability, tending thereby toward a constant total effect. However, when food availability is low, the added costs of basal metabolism and external work relative to assimilation may have a pronounced effect on growth efficiency.

When one turns from consideration of the individual and its physiological growth efficiency to the "ecological efficiency" of food conversion from one trophic level to the next (*2*, *29*), there are additional losses to be taken into account. Any of the food consumed but not assimilated would be included here, though it is possible that undigested organic matter may be reassimilated by members of the same trophic level (*2*). Any other nonassimilatory losses, such as losses due to natural death, sedimentation, and emigration, will, if not otherwise accounted for, appear as a loss in trophic efficiency. In addition, when one considers a specific or selected part of a trophic level, such as a population of fish of use to man, the consumption of food by any other hidden member of the same trophic level will appear as a loss in efficiency. For example, the role of such animals as salps, medusae, and ctenophores in marine food chains is not well understood and is seldom even considered. Yet these animals may occur sporadically or periodically in swarms so dense that they dominate the plankton completely. Whether they represent a dead end or side branch in the normal food chain of the sea is not known, but their effect can hardly be negligible when they occur in abundance.

Finally, a further loss which may occur at any trophic level but is, again, of unknown or unpredictable magnitude is that of dissolved organic matter lost through excretion or other physiological processes by plants and animals. This has received particular attention at the level of primary production, some investigators concluding that 50 percent or more of the photoassimilated carbon may be released by phytoplankton into the water as dissolved compounds (*30*). There appears to be general agreement that the loss of dissolved organic matter is indirectly proportional to the absolute rate of organic production and is therefore most serious in the oligotrophic regions of the open sea (*11*, *31*).

All of the various factors discussed above will affect the efficiency or apparent efficiency of the transfer of organic matter between trophic levels. Since they cannot, in most cases, be quantitatively estimated individually, their total effect cannot be assessed. It is known only that the maximum potential growth efficiency is about 30 percent and that at least some of the factors which reduce this further are more pronounced in oligotrophic, low-productivity waters than in highly productive situations. Slobodkin (*29*) concludes that an ecological efficiency of about 10 percent is possible, and Schaeffer feels that the figure may be as high as 20 percent. Here, therefore, I assign efficiencies of 10, 15, and 20 percent, respectively, to the oceanic, the coastal, and the upwelling provinces, though it is quite possible that the actual values are considerably lower.

Conclusions and Discussion

With values assigned to the three marine provinces for primary productivity (Table 2), number of trophic levels, and efficiencies, it is now possible to calculate fish production in the three regions. The results are summarized in Table 3.

These calculations reveal several interesting features. The open sea—90 percent of the ocean and nearly three-fourths of the earth's surface—is essentially a biological desert. It produces a negligible fraction of the world's fish catch at present and has little or no potential for yielding more in the future.

Upwelling regions, totaling no more than about one-tenth of 1 percent of the ocean surface (an area roughly the size of California) produce about half the world's fish supply. The other half is produced in coastal waters and the few offshore regions of comparably high fertility.

One of the major uncertainties and possible sources of error in the calculation is the estimation of the areas of high, intermediate, and low productivity. This is particularly true of the upwelling area off the continent of Antarctica, an area which has never been well described or defined.

A figure of 360,000 square kilometers has been used for the total area of upwelling regions in the world (Table 2). If the upwelling regions off California, northwest and southwest Africa, and the Arabian Sea are of roughly the same area as that off the coast of Peru, these semitropical regions would total some 200,000 square kilometers. The remaining 160,000 square kilometers would represent about one-fourth the circumference of Antarctica seaward for a distance of 30 kilometers. This seems a not unreasonable inference. Certainly, the entire ocean south of the Antarctic Convergence is not highly productive, contrary to the estimates of El-Sayed (*32*). Extensive observations in this region by Saijo and Kawashima (*33*) yielded primary productivity values of 0.01 to 0.15 gram of carbon per square meter per day—a value no higher than the values used here for the open sea. Presumably, the discrepancy is the result of highly irregular, discontinuous, or "patchy" distribution of biological activity. In other words, the occurrence of extremely high productivity associated with upwelling conditions appears to be confined, in the Antarctic, as elsewhere, to restricted areas close to shore.

An area of 160,000 square kilometers of upwelling conditions with an annual productivity of 300 grams of carbon per square meter would result in the production of about 50×10^6 tons of "fish," if we follow the ground rules established above in making the estimate. Presumably these "fish" would consist for the most part of the Antarctic krill, which feeds directly upon phytoplankton, as noted above, and which is known to be extremely abundant in Antarctic waters. There have been numerous attempts to estimate the annual production of krill in the Antarctic, from the known number of whales at their peak of abundance and from various assumptions concerning their daily ration of krill. The evidence upon which such estimates are based is so tenuous that they are hardly worth discussing. It is interesting to note, however, that the more conservative of these estimates are rather close to figures derived independently by the method discussed here. For example, Moiseev (*34*) calculated krill production for 1967 to be 60.5×10^6 tons, while Kasahara (*3*) considered a range of 24 to 36×10^6 tons to be a minimal figure. I consider the figure 50×10^6 tons to be on the high side, as the estimated area of upwelling is probably generous, the average productivity value of 300 grams of carbon per square meter per year is high for a region where photosynthesis can occur during only half the year, and much of the primary production is probably diverted into smaller crustacean herbivores (*35*). Clearly, the Antarctic must receive much more intensive study before its productive capacity can be assessed with any accuracy.

In all, I estimate that some 240 million tons (fresh weight) of fish are produced annually in the sea. As this figure is rough and subject to numerous sources of error, it should not be considered significantly different from Schaeffer's (*2*) figure of 200 million tons.

Production, however, is not equivalent to potential harvest. In the first place, man must share the production with other top-level carnivores. It has been estimated, for example, that guano birds alone eat some 4 million tons of anchovies annually off the coast of Peru, while tunas, squid, sea lions, and other predators probably consume an equivalent amount (*22*, *36*). This is nearly equal to the amount taken by man from this one highly productive fishery. In addition, man must take care to leave a large enough fraction of the annual production of fish to permit utilization of the resource at something close to its maximum sustainable yield, both to protect the fishery and to provide a sound economic basis for the industry.

When these various factors are taken into consideration, it seems unlikely that the potential sustained yield of fish to man is appreciably greater than 100 million tons. The total world fish landings for 1967 were just over 60 million tons (*37*), and this figure has been increasing at an average rate of about 8 percent per year for the past 25 years. It is clear that, while the yield can be still further increased, the resource is not vast. At the present rate, the industry can continue to expand for no more than a decade.

Most of the existing fisheries of the world are probably incapable of contributing significantly to this expansion. Many are already overexploited, and most of the rest are utilized at or near their maximum sustainable yield. Evidence of fishing pressure is usually determined directly from fishery statistics, but it is of some interest, in connection with the present discussion, to compare landings with fish production as estimated by the methods developed in this article. I will make this comparison for two quite dissimilar fisheries, that of the continental shelf of the northwest Atlantic and that of the Peruvian coastal region.

According to Edwards (*38*), the continental shelf between Hudson Canyon and the southern end of the Nova Scotian shelf includes an area of 110,000 square miles (2.9×10^{11} square meters). From the information in Tables 2 and 3, it may be calculated that approximately 1 million tons of fish are produced annually in this region. Commercial landings from the same area were slightly in excess of 1 million tons per year for the 3-year period 1963 to 1965 before going into a decline. The decline has become more serious each year, until it is now proposed to regulate the landings of at least the more valuable species such as cod and haddock, now clearly overexploited.

The coastal upwelling associated with the Peru Coastal Current gives rise to the world's most productive fishery, an annual harvest of some 10^7 metric tons of anchovies. The maximum sustainable yield is estimated at, or slightly below, this figure (*39*), and the fishery is carefully regulated. As mentioned above, mortality from other causes (such as predation from guano birds, bonito, squid, and so on) probably accounts for an additional 10^7 tons. This prodigious fishery is concentrated in an area no larger than about 800 × 30 miles (*36*), or 6×10^{10} square meters. By the methods developed in this article, it is estimated that such an upwelling area can be expected to produce 2×10^7 tons of fish, almost precisely the commercial yield as now regulated plus the amount attributed to natural mortality.

These are but two of the many recognized examples of well-developed commercial fisheries now being utilized at or above their levels of maximum sustainable yield. Any appreciable continued increase in the world's fish landings must clearly come from unexploited species and, for the most part, from undeveloped new fishing areas. Much of the potential expansion must consist of new products from remote regions, such as the Antarctic krill, for which no harvesting technology and no market yet exist.

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