cological studies of rubidium and related cations, such as cesium, with possible evaluation for their use in depressive states.

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How Much Food from the Sea?

We have read with interest John H. Ryther's recent article "Photosynthesis and fish production in the sea" (*1*). Ryther's estimate of annual fish production (about 100 million tons) falls within the range (80 to 2000 million metric tons) estimated in the past few years by other scientists (*2*). It is, however, at the lower end of this range. The importance of his contribution must be viewed in the light of whether or not his work provides a better focus on the yield of fishes that may be anticipated from the world's ocean.

The technique used by Ryther and other scientists who have derived estimates based on the flow of material through the food chain involves three primary considerations: the amount of carbon fixed annually; the efficiency with which nature transfers material up through the food chain; and the trophic level selected for calculating fish production or yields. Apart from the uncertainty surrounding the total amount of oceanic carbon fixed, such estimates of potential fish production are based (i) on the assumption that the complex and variable food web in the sea can be treated as a simple chain of trophic levels and that fish production can be assigned to a specific level in the chain, (ii) on the belief that it is possible to reduce the variable values for efficiency of transfer of material from predator to prey to a single set of values representing ecological efficiency, and (iii) on a guess as to the percentage of production at present available to man.

Estimates obtained by this technique are extremely sensitive to the values assigned these parameters. Ryther's table 1 (*1*) represents a matrix of ecological efficiency and trophic levels. The choice between two adjacent levels involves a possible error of an order of magnitude or more, depending on the ecological efficiency factor chosen. The choice within a given range of ecological efficiencies involves error factors ranging from approximately 2 to 15. Even when other sources of uncertainty are ignored, Ryther's estimates could easily be in error in either direction by a factor of 1 to 2 orders of magnitude.

The sensitivity of this technique for estimating fish production has been recognized by most workers who have used it. Ryther departs from his predecessors in that he categorizes the ocean into "provinces," using relative primary productivity as a criterion, and subsequently examines the potential fish harvests of these provinces. His relatively low figure for total potential production of fish results from his selection of the third and fifth trophic level in calculating fish production from the coastal and oceanic provinces, respectively, and from the small total area suggested for the upwelling province.

Ryther presents little explanation for his use of trophic levels three and five steps removed from primary production for the coastal and ocean areas. We doubt that there are any plankton ecologists who would agree "that virtually all the copepods, many of which are themselves carnivores, must be preyed upon by chaetognaths," even in the open ocean. For fishes in general, Ryther follows the logic of other biologists who have based trophic levels on the feeding habits of adult forms only. In many species, including the tunas and dolphins, the greatest net growth of the population occurs during the early life history of the species. It is common for many species of fish to attain the maximum weight potential before the species reaches maturity and relatively early in its life span. In fact, for adults, the weight added to the population in any time period is often exceeded by losses due to natural mortality. Thus, adults degrade net productivity rather than add to it. Fishing normally will change the population structure toward smaller sizes which have a higher ecological efficiency and which feed on organisms lower in the food chain. At any rate, there is considerable evidence that some important pelagic fishes feed on invertebrates which are largely herbivorous. For example, over a great part of the eastern tropical Pacific the summer diet of adult yellowfin tunas (*Thunnus albacares*) is dominated by the herbivorous pelagic crabs *Pleuroncodes planipes* (*3*).

Also, the works of other authors suggest that the number of trophic levels proposed by Ryther may be too high. Blackburn (*4*) suggests two fewer links than Ryther does for the chain of trophic levels between phytoplankton and man in the open ocean environment of the tuna fisheries. Steele (*5*) has shown that the observed fish catches in the North Sea could be supported by primary production only if the fish were feeding mainly at the second trophic level (not at the third, as suggested by Ryther). Since Steele's paper was written, North Sea catches have been increased to over 3 million metric tons, in 1967 and 1968, or to more than 5 ton/km^2—well above Ryther's estimate of total production.

On examining Ryther's table 3 (*1*), it becomes obvious that a small error in calculated productivity could make a considerable difference in the final estimates. For example, in recent work the English scientist Cushing (*6*) suggests a much greater size for the area of rich upwelling water than Ryther does. Ryther admits the possibility of error regarding this matter.

There are, however, some discrepancies in the figures given by Ryther for upwelling. For example, the observed production of fish off Peru will agree with his estimates if the area of productive upwelling off Peru is, as he states (*1*, p. 76), 60×10^3 km^2, but the observed production is much too high if the area is 36×10^3 km^2, as is implied on page 73 of his article. If we take the upwelling zone figures (60×10^3 km^2) used by Ryther (*1*, *76*), and if the total upwelling area is, as stated, 10 times the upwelling area off Peru, the fish production in the upwelling province would be 200 million metric tons, not 120. Other numerical errors in the text make it difficult to evaluate the importance of Ryther's contribution, as they may alter his own conclusions. For example, the 1967 catch of oceanic fishes was 46.9×10^6 tons, rather than 60×10^6 as Ryther implies, and the estimate of krill production, taken from Moiseev (*7*), is misquoted. The figure 60.5 million metric tons is the total world fish catch for 1967. Moiseev did not, in his article, estimate annual krill production, but he estimated the krill consumption of the unexploited whale stocks to be 150 million tons in a 3- to 4-month period. Similarly, Kasahara (*8*) did not estimate the minimum total annual krill production to be "24 to 36 $\times 10^6$ tons," as Ryther states, but estimated that the consumption by fin whales alone during summer months at least equaled this figure.

On the last page of his article Ryther discusses the fish catch in a 110,000-square-mile area between Hudson Canyon and the southern end of the Nova Scotian shelf and relates it to 1 million tons of fish that would theoretically be *produced* annually (according to the material-flow analyses). He then states that the area *yielded catches* that were slightly in excess of 1 million tons per year during the period 1963 to 1965 and subsequently declined. The catch figures given by Ryther are confusing. The catches from this region during the period denoted were closer to 1.7 million tons annually. Further, the catches did not decline after 1965. During the 3-year period 1966 to 1968, the average annual catch (about 1.8 million tons) was greater than it was during the period 1963 to 1965, and no discernible trend is apparent.

Since only a part of fish production is available for catch by man (somewhat less than half, according to Ryther's approximation), one must conclude that catches during the 6-year period 1963 to 1968, as well as being about 1.7 times the *total production* forecast by Ryther, were more than 3 times the amount which might be caught! The example lends little support to his argument. Edwards (*9*), whom Ryther cites as the source of his figures on the size of the area involved, forecast a total production potential of 2 million tons annually from the same region if a "highly organized, versatile, efficient fishery" were operating. This forecast appears to be more reasonable in light of the performance of the fishery.

We are not aware of any proposed regulation to reduce fishery pressure on cod, such as Ryther suggests, and there has been no decline in catches of this species. The 1968 catch of cod from the 110,000-square-mile area defined above was almost double the 1963 catch, and there was a sharp upward trend over the period 1963 to 1968.

If one looks at Ryther's estimated production for the oceanic province (1.6×10^6 tons) and compares it with the catch of tunas, bonitos, and dolphins, there appears to be reason to doubt the validity of his description of the ocean as essentially a "biological desert." The catch of tunas, bonitos, skipjacks, and billfishes over the 3-year period 1965 to 1968 was roughly 1.4 million tons (*10*). This catch is derived from wide areas extending across the tropical Pacific and from the more temperate waters to the north and south of this zone, and also from similar regions of the Indian and Atlantic oceans. A small part of this catch could be attributed to the coastal and upwelling province. The catch of this group of pelagic fishes, however, almost equals the total production forecast for the ocean province. As only a part of fish production is available to man, we come to the conclusion that the pelagic fishes noted above have catch yields about twice as high as those suggested by Ryther's data. If we add the catches of other pelagic fishes taken from the high seas, we find the yield from the oceanic province to be currently between 2½ and 3 million tons annually, an actual catch about 3 times that suggested by Ryther (*1*, table 3).

Ryther, in the last paragraph of his article, states that much of the potential expansion must consist of "unexploited species" from remote regions, "such as the Antarctic krill, for which no harvesting technology and no market yet exist." The possibility of harvesting organisms not conventionally used as food cannot be dismissed lightly. In the waters adjacent to Japan, over a half million tons of squid were caught in 1967; krill have been harvested in the Antarctic by the Soviets for several years and are being marketed in the Soviet Union; and lantern fish are being harvested off South Africa (*11*), where they are commercially attractive because of their high oil yield.

Unlike Ryther, we believe that the question of potential fish production can be best answered through a more pragmatic approach based on knowledge of present commercial fish stocks and on extrapolation from exploratory surveys and other direct evidence. The United Nations, under the auspices of the Food and Agriculture Organization, is now in the process of evaluating data in an attempt to estimate the potential harvest of fish from the world's oceans. These studies are not yet completed. However, the estimated annual harvest of just three groups of fish—the large pelagic fishes of the open ocean (such as tunas and salmon), the larger species of bottomfish (such as cods and flounders), and the schooling pelagic fishes (such as herring and anchovies)—will amount to well over 100 million metric tons. To this we must add the crustaceans, the mollusks (including cephalopods), and a whole range of small fishes whose potential as food appears larger by perhaps an order of magnitude than that of better-known fish.

It seems to us that Ryther's article has done little to resolve the current arguments concerning the potential of the oceans as a source of food, and that his dramatic conclusions that at its present rate the fishing industry can continue to expand for no more than a decade and that the present yield of fish for man is not appreciably greater than 100 million tons annually are unwarranted. His selection, for his calculations, of relatively high trophic levels from the coastal and ocean province is questionable. The areas of high productive upwelling are not yet well known (as Ryther admits), and the correlative examples that he gives do not support his case. In fact, they detract from it. We can expect, however, that the article will stimulate further debate on this issue which may help us eventually to solve the puzzle. In the end, Ryther may be right but for the wrong reason. If the world catch of sea fish levels off in the next decade, this is likely to be due to the collapse of major fisheries because of climatic cycles, to overfishing, to oceanic pollution, to a failure to resolve problems of international jurisdiction, or to a combination of these factors rather than to inadequacy of unexploited resources.

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In my article (*1*) I estimated a total fish production in the sea of 240 million metric tons, rounding this figure to 200 million tons to make it compatible with earlier estimates, of Schaefer and others, from which I felt my number did not differ significantly. I then suggested that roughly half that amount, or about 100 million tons, would be available to exploitation by man. I had thought that these figures were rather widely accepted, at least by the more responsible if somewhat more conservative members of the profession. I am still not sure whether it is the estimate tself or simply the audacity of a nonishery biologist in making such an stimate that has been challenged by lverson, Longhurst, and Gulland.

Alverson, in a recent paper (*2*), comiled a table which included 17 estiates of annual fish production in the a. Of these, all but two were 200 miln tons or less and all but six were 5 million tons or less. The statement that my estimate "falls at the lower end of the range" is therefore not correct.

I had considered my estimate of the potential yield of the entire ocean neither original nor very interesting. Where I had hoped that my contribution to originality might lie was in the breakdown of the potential yield into the three regions or "provinces" of the ocean, showing that most of the fish are produced in a very small area and that most of the ocean is biologically impoverished. To this concept Alverson *et al.* do not address themselves in any serious way. Some of their comments are certainly correct; others seem illogical. (For example, the statement "It is common for many species of fish to attain the maximum weight potential before the species reaches maturity and relatively early in its life span" seems to say that many species attain maximum weight before they are full-grown. The sentence that follows—"In fact, for adults, the weight added to the population in any time period is often exceeded by losses due to natural mortality"—would appear to imply that adult fish cannot persist in the population, since they are dying faster than they are being recruited.) None of the comments affect the basic argument of my paper.

Several of the literature citations are quoted out of context or are otherwise misleading. Let me give three examples. Cushing, obviously using quite different criteria, did in fact identify a much larger total area of upwelling than I did. He went on to conclude, however: "Taking all upwelling areas, the production of fish and squid may be as much as 120–130 million tons. If we assume that one-third to one-half can be taken by fishing, then a potential catch of 40–60 million tons is available." My estimate, before rounding of numbers, was a production of 120 million tons from all the upwelling regions, of which half, or 60 million tons, might be available to fishing.

I was mistaken in including cod among the species of the Northwest Atlantic that have been designated for regulation. Only haddock, after its near extinction, has belatedly received that protection. It is interesting, however, to compare the rather optimistic statement of Alverson *et al.* concerning that fishery with a statement of R. L. Edwards (whom they cite): "This increased exploitation has had its direct effects. Some of the fisheries are out of business; others are barely maintaining themselves. . . . The scientific evidence is clear cut. The overall abundance of those species taken with an otter trawl has dropped 40% in four years." The years in question are 1964 to 1967. In the same paper Edwards quotes H. W. Graham, director of the Bureau of Commercial Fisheries Laboratory in Woods Hole, as follows: "Our conclusion at the moment is that the Northwest Atlantic on the whole is in a heavily exploited state and that we cannot expect any substantial increase from the area in the future." And Gulland himself has recently stated (*3*), "At the time of the United Nations Scientific Conference on the Conservation and Utilization of Resources held in 1949 at Lake Success . . . the Conference produced a map showing some 30 stocks then believed to be underfished. Of these stocks about half are now in need of proper management, including cod, redfish, and herring in the North Atlantic. . . ."

Finally, Alverson *et al.* refer to the effort by the Food and Agriculture Organization of the United Nations to estimate the potential harvest of fish from the world's oceans, implying that its study, when completed, will result in an estimate much higher than mine. The Committee on Fisheries of FAO, who were responsible for this study, issued a report in April 1969 (*4*) that included a table with the heading, "Fish catch (1965) and estimated world potential by marine area and species." The species headings are "large pelagic," "demersal," "shoaling pelagic," "cephalopods," and "crustaceans." The total world potential given in this table is 120 million tons, precisely the same as my estimate before rounding the numbers. True, the committee did not include "a whole range of small fishes" not presently harvested. Neither did I, on the assumption that such species are too small and too widely dispersed in the sea to be economically harvestable and useful to man, and that, in fact, they are a part of the food chains that support those larger species already being utilized.

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