

FOOD CHAINS AND FISHERIES: AN ASSESSMENT AFTER 20 YEARS

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ABSTRACT. Oceanic food chain research has been notably unsuccessful in predicting fish yield, chiefly because of inadequate methods for determining primary production and for the lack of data on transfer efficiencies between steps in food chains. Methods have improved in recent years in assessing primary production (both recycled and new) but the state of the science does not yet permit grand means of primary production to be assigned to the world's oceans nor for them to be used to predict fisheries yield.

1. INTRODUCTION

Almost 20 years ago, at the 1968 symposium on marine food chains (Steele, 1970) I presented data to show that it was impossible to maintain the 1932-33 population of sardines of about 3,000,000 metric tons (mtons) in the California Current with the primary production measured for the California Current and inshore waters where the sardine resides (Lasker, 1970). My data source for primary production was the late John D.H. Strickland who provided me with his most up-to-date estimate ($1gC/m^2$ per day) of primary production for the area where sardines were found. These data were subsequently published (Eppley *et al.*, 1970). Sardines are zooplankton feeders and therefore they were at the top of a two step food chain. I used a conversion efficiency of 10% between steps in the food chain.

In the final analysis, there was no accounting for sustaining the large biomass with the primary production measured in the sardine's habitat. At that time I speculated that the sardine biomass may have been estimated at too high a level, or the estimates for primary and secondary production were too low.

Food chain research has contributed more to the knowledge of biogeochemical cycles in the ocean and to describing the driving forces behind the sinking flux of biogenic particles than to fisheries science in recent years. Primary production may not be the most important environmental variable for fish stocks. This is suggested by poor correlations between primary production and fish biomass and the fact that aggregations of food rather than total integrated food may

be more important to larval fish survival (Lasker, 1975). Nevertheless at some level there must be a reckoning between the energy requirements of fish and the production of their food.

In this paper I reexamine this problem in light of the latest data available, examine other biological systems and try to come to some conclusion whether Food Chain Research has made a contribution to Fisheries Science.

2. THE PRIMARY PRODUCTION CONTROVERSY

For some time there has been general unhappiness among biological oceanographers with the Carbon-14 method of primary productivity measurements (Peterson, 1980). Studies of oxygen distribution in the north Pacific by Shulenberg and Reid (1981) have also cast doubt on previous work done in the "deserts of the sea" on primary production. They suggested that measurements of oxygen trapped below the surface layers of nutrient-poor oligotrophic regions, were evidence of an amount of primary production, heretofore not measured, and two to four times as much as ever reported for these areas throughout the world. Jenkins (1982) and Jenkins and Goldman (1985) came to similar conclusions based upon oxygen distributions in the north Atlantic. Recent measurements on the CO₂ system also seem to support the concept of extra oxygen production and unmeasured primary production (Brewer, *et al.* 1986, and Pers. Comm.).

Notwithstanding the argument by Platt (1984) and Platt and Harrison (1986) who see errors in interpretation and magnitude in the subsurface oxygen hypothesis, the ocean science community may have been underestimating primary production by some multiple in the open ocean (Kerr, 1983) and by some smaller fraction in inshore waters.

Toxicity of samplers and incubation bottles has been implicated in depressing the amount of carbon incorporation in the carbon-14 technique (Fitzwater *et al.*, 1982). The trace metal "clean" methods of these authors appear to have resolved much of the problem and have been used in recent U.S. National Science Foundation programs aimed at improving primary production measurements.

3. RYTHER'S 1966 PAPER ON FISH PRODUCTION

The paper by Ryther (1966) is a good example of the extent to which primary production figures have been used in calculations on fish yield. Ryther divided the world's oceans into open ocean, coastal, and upwelling regions, then assigned 5, 3 and 1.5 trophic levels and 10, 15 and 20% efficiencies of transfer respectively, leading to the production of fish.

Based on productivity figures compiled and published by Russian scientists (Koblentz-Mishke, *et al.* 1970; this was In Press in 1969) and Steemann Nielsen and Jensen, (1957) using the Steemann Nielsen (1957) technique of Carbon-14 incorporation into phytoplankton, Ryther deduced that primary production would be at its maximum at 20×10^9

mtons of carbon per year in the world and that the world fish production can be only about 24×10^7 mtons (wet weight) per year. From this figure he concluded that the world's commercial fish maximum sustainable yield could not exceed 10×10^7 mtons per year.

Fishery biologists were quick to dispute Ryther's conclusions but chiefly his low estimate of what tropical oceans can produce in fish. Alverson *et al.* (1970) argued with Ryther's conclusion that 90% of the ocean is a "biological desert." They pointed out that it did not square with the fact that the yield in tunas, billfishes and other open ocean pelagic fishes in the mid 1960s was 2.5 to 3×10^6 mtons annually, as against Ryther's estimate of only 1.6×10^6 mtons per year total fish production. The tuna and billfish catch alone exceeded 2.2×10^6 mtons in 1984, the last year for which statistics were compiled (FAO, 1986). To make their case, Alverson *et al.* (1970) included "tuna-like" fishes, many of which occur in coastal and upwelling regions, although they argued that it made no difference to their case.

In fairness to Ryther, he made the conservative assumption that there are most likely 5 steps in the food chain in the open ocean, as opposed to about 1.5 in upwelling systems, and used a reasonable 10% efficiency in energy transfer between steps in the open ocean. The four to five step food chain has been verified by Mearns *et al.* (1981) and Rau *et al.* (1983). The important point to be made however is that Ryther calculated a maximum sustainable yield for fisheries for all the world's oceans of 100 million mtons. This maximum was the major point of contention from fishery scientists. Alverson *et al.* (1980) were convinced this was too low. A recent paper by Wise (1984) makes the point that 100-120 million mtons limitation may only be due to fishing practices and consumer acceptance. He leaves his readers with the impression that all previous prognostications of status quo for world fisheries (e.g. United States, 1980) have been mistaken and will continue to underestimate harvests from the sea. We have very reliable statistics on the world marine fish catch which show that the tuna and billfish catch has been increasing since 1968 by 70000 mtons per year and for all marine fish by 1.5×10^6 mtons per year for the last 35 years (FAO, 1986) and this has been one of the causes for the optimism of fishery scientists.

A recent estimate of primary production for the global ocean is 51×10^9 mtons of carbon per year (Martin *et al.*, 1987). The mean productivity rates for the open ocean, coastal zone and upwelling areas of Martin *et al.* exceed those summarized by Ryther (1969) by factors of 2.6, 2.5 and 1.4 respectively. All but about 7×10^9 mtons of this production is recycled in the upper 100 m by processes including fish metabolism. The fish catch itself is an export from the productive system of the surface ocean and thus cannot exceed global "new production" (Dugdale and Goering, 1967). Global new production is probably about 20% of the total. A recent estimate of new production in the equatorial Pacific alone is 1×10^9 mtons per year (Chavez and Barber, 1987). Global new production is well in excess of the fish catch but the fate of most of this new production is to end up as biogenic particles in the depths of the sea (Eppley and Peterson,

biogenic particles in the depths of the sea (Eppley and Peterson, 1979).

The uncertainties of Ryther's educated assumptions and the importance of correct figures in predicting the world fish catch have been an impetus to food chain scientists to make the pertinent measurements more accurate and therefore to obtain more reliable production values for the world's oceans. Should the fishing community view the future with unbridled optimism or is the leveling off of world fisheries just a matter of a few years' time?

4. WHAT CARBON INCORPORATION FIGURES TO USE?

For the coastal Pacific sardine, (*Sardinops sagax* - *S. caeruleus*), we have population figures from California and Baja California fishery data (Murphy, 1966 and MacCall, 1979). At its maximum, in 1932-33, the subpopulation centered in the Southern California Bight was 3.2 million mtms. The energy required for respiration by this population was 2.8×10^{12} Kcal/month, and the population required an intake of 2.2×10^{11} g C/month (Lasker, 1970).

The area covered by this population was 4.14×10^{10} m². At 1g/m²C produced for a 30 day month, the primary production for this area is calculated to be 1.24×10^{12} gC/month.

Primary production.	1.24	x	10^{12} gC/month
Zooplankton production.	0.124		"
Sardine respiration.	0.22		"

These results are not substantially different from what I reported in 1970. Ryther used a 20% efficiency figure between phyto- and zooplankton while I used 10%. On the other hand I used 1gC/m² per day as a best estimate of coastal productivity and now the figure, derived from many more Carbon-14 measurements, is best put at 0.5g C/m² per day for the inner Southern California Bight (Smith and Eppley, 1982) while higher values are found offshore in the California Current (Hayward and Venrick, 1984). When the Ryther and Smith and Eppley figures are used, the calculation is:

Primary Production.	0.62	x	10^{12} gC/month
Zooplankton production.	0.12		"
Sardine Respiration.	0.22		"

Despite the 2X discrepancy between calculated zooplankton production and the amount of carbon needed to support the 3 million mtms of sardines, the figures are as good as we can expect given the present state of knowledge of primary production and transfer efficiency in the coastal zone, the lack of information on secondary production, and the errors in fish population estimation. For example, in estimating the sardine population, Murphy (1966) used an assumed natural mortality (M) figure of 0.5. Had he used 0.4 the estimated biomass would have been about 20% higher.

It also seems likely that to the north, off central and northern California, the highly energetic "jets and squirts" which move large quantities of cold, nutrient-enriched water offshore and become entrained into the southward moving California current (Lasker, et al., 1981; Treganza et al., 1987) add more primary production to the habitat of the sardine than has been included in the gross overall average. For the sardine and other fauna of this region it seems that we have achieved about the best input-output balance for the population if we agree that there are still uncertainties in our understanding of transfer efficiencies and in the methods and time scales of sampling used to measure primary production, and that there are probably nutrient inputs not yet accounted for. A promise of satellite technology is that we may acquire in the future much more comprehensive information on phytoplankton production on synoptic scales (Eppley et al. 1985).

5. OTHER UPWELLING SYSTEMS

While the northern and central parts of the California coast are areas of intense upwelling, with the production of jets and squirts bringing in as yet unmeasured quantities of nutrients, the Peruvian upwelling system by contrast supports much greater populations of fish, particularly the Peruvian anchoveta, *Engraulis ringens* and the Chilean sardine, *Sardinops sagax*. At its height the spawning biomass of the Peruvian anchoveta exceeded 20 million mtons (Csirke, 1980; Tsukayama, 1982) and the catch alone in 1968 was greater than 12 million mtons. The anchoveta is a phytoplankton feeder and the one-step food chain undoubtedly helped make this remarkable upwelling system more productive of fish. A 20 million ton anchoveta population has a carbon intake rate of approximately 6.8×10^{13} gC/yr based on the respiration measurements of Villavicencio (1981) where the Peruvian anchoveta has a total metabolic requirement of 87.2 cal./g per day. The conversion of calories to carbon is based on the combustion of glucose where 1g C yields 9350 calories. Chavez and Barber (1987) conclude from their study that 1409 gC/m^2 per year are produced in the Peruvian upwelling zone (3.84 gC/m^2 per day) and that the area of that zone is $1.82 \times 10^{11} \text{ m}^2$. The total production was calculated to be 2.6×10^{14} gC per year, 40 times more than required by a 20 million ton anchoveta population. These exercises serve to illustrate that, at least in upwelling areas, the correspondence between carbon production measured and that needed by large fish populations is within reasonable bounds. Whether the discrepancies are due to primary production measurements or the area to which they are applied, other inaccuracies, e.g. estimating the biomass of large fish populations, the utilization of phytoplankton by other organisms, or extrapolation of laboratory oxygen consumption figures to caloric needs of field populations, cannot be stated at this time, and indeed these may be unanswerable questions.

6. FISH POPULATIONS IN "OLIGOTROPHIC" SEAS

Olson and Boggs (1986) have produced a significant work in their study of the apex predator, *Thunnus albacares*, the yellowfin tuna of the eastern tropical Pacific Ocean. This species is abundant throughout the world's tropical seas and may typify the abundances of the major apex predators in the open ocean. Sharp and Francis (1976) estimated an unexploited population of about 600,000 mtons was required to support the yellowfin surface fishery of 1966-71. Olson and Boggs used a 300,000 mton estimate for 1970-72 standing stocks, which was calculated by Inter-American Tropical Tuna Commission scientists (Anon, 1986) to calculate predation rates of the population. By using the more conservative figure of 300,000 mtons, an annual consumption of 4.5×10^9 kg of forage ($= 1.24 \times 10^{12}$ gC) and 5 steps in the food chain (Mearns et al., 1981; Rau et al. 1983) with an efficiency between steps of 10%, we find that for the area of the yellowfin tuna habitat, 1.7×10^{13} m², 730gC/m² primary production per year are needed or approximately 2gC/m² per day over the whole area. This has to be an underestimate since no other top predators are included in the biomass. The most recent (1985) biomass estimate for yellowfin tuna in this area is 450,000 mtons, the result of a post-El Niño succession of three exceptional year classes (Anon. 1986).

Feldman (1986) has shown that the productive area of the eastern tropical Pacific has varied an order of magnitude between years based on satellite chlorophyll images. Dandonneau (this volume) using extensive ship-of-opportunity data, confirmed and extended these observations to the southwestern tropical Pacific and suggested a mechanism for this increased production. Cooling of the surface layer in the winter increases the depth of the mixed layer which overturns and brings up nitrate from the deep.

Owen and Zeitschel (1970) showed a seasonal change in primary production for this region using the Carbon-14 method, from 127 mg/m² per day to 318 mg/m² per day, or an average annual production of 75g/m², an order of magnitude lower than needed by this population of yellowfin tuna as calculated using the 10% transfer efficiency and the excellent data on forage requirements by Olson and Boggs (1986), but slightly more than the rate used by Ryther (50g C/m² per year) to make his calculations.

Between 90° and 180°W in the equatorial tropical Pacific is an oceanic upwelling zone which is unusually productive for open ocean areas. Ryther (1969) included areas like this in the estimate of 100gC/m² per year for the coastal zone (but not upwelling zone) production. Chavez and Barber (1987) suggest that the oceanographic upwelling zone of the tropical Pacific produces about 197gC/m² per year, about twice what Ryther estimated. While not an order of magnitude higher, the vast area over which this production occurs leads to the conclusion that populations in nearby areas, such as the yellowfin tuna in the eastern tropical Pacific, must benefit from this production.

Another possible mechanism for enhancing production in oligotrophic areas is nitrogen fixation. Blue-green algae in tropical

seas have been estimated to fix 5×10^6 mtons annually (Carpenter, 1983). It is difficult to put this figure in perspective because of the uncertainty of the amount of total new nitrogen available in tropical seas.

7. CONCLUSIONS

Marine food chain research seems still to be in its infancy when it comes to energy budgets. The numbers being generated for primary production are constantly being upgraded and the trend has been toward substantial increases for all areas of the world's oceans. Other new findings also increase the values to be used in calculations of ocean productivity. These are 1) the determination of markedly increased production by equatorial upwelling areas as well as the size of those areas (Chavez and Barber, 1987), 2) nutrient enrichment by jets and squirts of the coastal zone, 3) nutrient enrichment by eddy entrainment (Simpson, 1986), 4) nutrient enrichment by deepening and overturning the mixed layer in tropical seas (Dandonneau, 1987), 5) the possibility of a utilizable pool of dissolved organic nitrogen in "oligotrophic" seas (Suzuki *et al.*, 1985), 6) the continuing technical improvements in the methods for determining primary production, and 7) new methods for the more accurate determination of fish biomass (Lasker, 1985).

Other problems, not very different than those discussed 20 years ago, will also have to be resolved. For example, too few data on secondary production and percent transfer of energy through steps in the food chain prevent the determination of grand means for different ocean regimes. We lack too the information on feedback mechanisms in food chains which may influence transfer efficiencies.

All of these points bring us to the obvious conclusion that ocean scientists are not yet in a position to determine what the yield of food from the sea will be for the foreseeable future. The exercises to do so thus far have been important in pointing out the major problems in determining the starting point (primary production) and where we end up (commercial fisheries). A conference of this kind in 10 years may be able to resolve some of these issues, but we cannot do it today.

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