Estimates of Trophic Efficiency, Based on the Size Distribution of Phytoplankton and Fish in Different Environments

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Timothy R. Parsons and Yuh-Ling Lee Chen (1994) Estimates of trophic efficiency, based on the size distribution of phytoplankton and fish in different environments. *Zoological Studies* **33**(4): 296-301. The trophic efficiencies of four fisheries were calculated on the basis of the size spectrum and productivity of both the phytoplankton and the fish. Results showed that for the Gulf of Alaska salmon fishery and the Strait of Georgia Pacific whiting fishery, the average ecological efficiency was 14.3% and 13.2%, respectively, for each step in the food chain. The Kaohsiung offshore fishery has the highest ecological efficiency of 16.2%. These results contrast with the Kaohsiung nearshore fishery, which has an average ecological efficiency of only 7.4%. This result could be explained in terms of eutrophication of the nearshore environment, which is known to lower trophic efficiency in aquatic habitats, or it could be due to overfishing in this area. The importance of calculating the trophic efficiency exponent lies both in being able to detect the overall effect of environmental or anthropogenic stress on a fishery, as well as in being able to use the exponent to calculate fishery production, from the size spectrum and productivity of the primary producers.

Key words: Primary productivity, Size spectra, Fisheries.

Sheldon et al. (1977 1982) proposed a method for calculating the production of different sized fish, based on the size spectrum and productivity of the phytoplankton of the same ecosystem. The authors assumed that the ecological efficiency (defined as the multiple of the ecotrophic efficiency and the growth efficiency) could be closely approximated from the transfer efficiency, which can be determined as the ratio of productivity at one trophic level Pi, to the productivity of the preceding level, Pp. Since productivity could be defined as $P = rS$, where r is the instantaneous growth rate and S is the standing stock, the transfer efficiency (E_T) was then defined as the ratio r_iS_i/r_pS_p. From size distributions of biomass in the ocean, the authors argued that, on a logarithmic grade scale, the proportion of biomass (S), in different size categories from plankton to fish, was approximately equal, the transfer efficiency could then be determined from the ratio r_i/r_p. Since

growth rate is proportional to size, it was further suggested that the transfer efficiency from one trophic level to another could be determined by the ratio $(D_i/D_p)^{-0.72}$, where the D_i and D_p are the equivalent spherical diameters of the predator in trophic level "i" and of the prey in trophic level "p" and the exponent (-0.72) is an empirically derived constant relating the growth rate of different sized organisms.

The assumption in the above discussion, that the distribution of biomass is approximately equal from plankton to fish, has been discussed by Platt and Denman (1978) among others (cf. Rogriguez and Mullin 1986, Sprules and Munawar 1986, Quinones and Platt 1994) and there is now a general consensus that the distribution of biomass actually declines as a power function of size, the slope of the size spectrum being -0.22 based on a scale of organism volume. This has the net effect of lowering the ecological efficiency as predicted

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from the size ratio of predator and prey given above from Sheldon et al. (1982). However, in actual studies on the size spectrum of plankton in lakes (Sprules and Munawar 1986) and in the ocean (Rodriguez and Mullin 1986) it was found that there was considerable variability in the slope of the biomass spectrum; this has led to a general conclusion that the descending slope might be in some cases defined by habitat and also subject to external factors, such as migration or pollution.

In the following discussion we determine the exponent which defines the ecological efficiency, based on differences in the size spectrum of primary producers and fish, in four quite different environments. They are (1) the Sub-arctic coastal waters of the Strait of Georgia (ca. 49°N and 124°W) where there is a local Pacific whiting (*Merluccius productus*) fishery, (2) the Gulf of Alaska, which is the principal area of production of the Pacific salmon migrating to the rivers of western Canada and the USA, (3) an offshore tropical fishery, and (4) a tropical coastal fishery, the latter two being based near the city of Kaohsiung in southern Taiwan (ca. 22°N and 121°E). They are influenced by the waters of the South China Sea and occasionally by the Kuroshio. The comparison of fisheries yield and primary production in these four areas is essentially a sensitivity test of the ecological efficiency exponent in Equation 1.

METHODS

The Primary producers

The size spectrum of primary producers in the Gulf of Alaska was taken from Fig. 1 in Parsons (1972), which shows that most of the biomass of phytoplankton consists of nanoplankton in the size range, 2 to 20 μm. The primary productivity of the Gulf was taken from Hobson (1980) as an average value of 80 gC/m^2/yr.

The size spectrum of phytoplankton in the Strait of Georgia was taken from Fig. 2 in Parsons et al. (1969) and from Harrison et al. (1983); both illustrate that most of the phytoplankton biomass in this coastal subarctic environment during the highly productive spring and summer months is dominated by large diatoms in the microplankton size range, 20 to 200 μm. The primary productivity of the Strait of Georgia was taken as 280 gC/m^2/yr from Harrison et al. (1983).

The primary productivity of the offshore waters of Kaohsiung was calculated at 196 gC/m^2/yr by

Hung et al. (1986). The primary productivity of nearshore coastal waters was determined by one of us (Y-L.L.Chen) using the ^{13}C technique; results showed a steep gradient of very high (ca. 8 gC/m^2/day) primary productivities near the shoreline at a 6 m depth, to lower values further offshore at a 30 m depth (ca. 1.8 gC/m^2/day) out to 12 nm (22 km), where the average primary productivity from Hung et al. (1986) was taken to be 0.54 gC/m^2/day. An equation for the decline in primary productivity from the coast (1 km from the shoreline) out to 22 km was then determined and the value for the primary productivity at 11 km offshore was taken as the average figure for this nearshore region. This value was determined to be 1.094 gC/m^2/day and was multiplied by 365 to give an annual production of 399 gC/m^2. Using a seasonal range for one offshore station of 0.25 to 1.8 gC/m^2/day (Y-L.L.Chen), one obtains a very similar mean of 1.03 gC/m^2/day. Since the largest range (from 8 to 0.25 gC/m^2/day) was geographic, the former value was used in approximating annual primary productivity.

The size range of phytoplankton in the tropical waters of southern Taiwan was determined by counting and sizing phytoplankton; the size of inshore particles, which contained small diatoms and flagellates, was in the range 2 to 20 μm, while offshore phytoplankton was dominated by *Synechococcus* sp. in the picoplankton size range, 0.2 to 2 μm.

Using the same grade scale of particle diameter as in Sheldon et al. (1977), the number of size grades occupied by the phytoplankton in each of the above size ranges was then determined and the geometric mean size of each range was used to calculate the size difference between the primary producers and the major fishery in each environment. These data are summarized in Table 1.

Fisheries data

Data on the size of salmon and the total annual productivity of adult salmon in the Gulf of Alaska were taken from Rogers (1987). In order to convert these weights to the same particle diameter grade scale used for the phytoplankton, it was assumed that the density of all salmon species was close to unity and that the average weight in grams at the time of harvest represented the average volume of the fish in cm^3. These average sizes were 1.75 kg for pink salmon (*Oncorhynchus gorbuscha*), 4.5 kg for chum salmon (*O. keta*), 3.5 kg for coho salmon (*O. kisutch*) and 2.5 kg for sockeye salmon

Table 1. Summary of data used to determine the trophic efficiency exponent

Location	Primary productivity (gC/m^2/yr)	Factor — C:wet weight	No. size classes Fish/Phytoplankon	Range and mean size phyto (μm)	fish (cm)	Area of production (km^2)	Average fish harvest × 2 (tons wet wt)	Calculated exponent — (x)
Strait of Georgia (Canada)	280	10	2/11	20-200 71.9	8.4-9.2 8.98	6,900	14,746	0.768
Gulf of Alaska	80	10	3/11	2-20 7.12	12.7-25.4 18	3.96 × 10^6	4 × 10^5	0.735
Kaohsiung (Taiwan) offshore 200 n mi	196	10	6/11	0.2-2 0.712	4-16 7.12	158 × 10^3	56,184	0.696
Kaohsiung (Taiwan) nearshore 12 n mi	399	10	4/11	2-20 7.12	4-10.1 6.34	7,885	1,466	0.985

(*O. nerka*). Chinook salmon (*O. tshawytscha*), which are much larger (9.5 kg) than the other four species and were not included in this calculation because they only make up about 5% of the total catch and their inclusion would distort the size spectrum in favor of a much larger mean salmon size than is represented by pink, sockeye, coho, and chum salmon. The equivalent spherical diameters were then calculated for four species of salmon and this gave a size spectrum ranging from 12.7 to 25.4 cm in three size classes with a mean diameter of 18 cm. The total production of salmon in the Gulf of Alaska was taken as 2.5 × 10^5 from Rogers (1987) as an average for the years l950 to l977 (approximately the same period over which the estimate of primary production was made by Hobson 1980).

In order to complete the calculation of fish production from primary production, an estimate was made of the total area of the Gulf of Alaska. Taking the general description of the Gulf from Hood (1987), it was estimated that the total area of the Gulf was about 3.96 million km^2 from the northern coast, west to 176°W and on an arc south down to where the 50°N line of latitude joins the coast of British Columbia, excluding from the estimation the immediate coastal regions of fjords and estuaries.

The equation from which the exponent (x) was then calculated for the Gulf of Alaska and for each of the three other fisheries is given as:

EQU-1 $P \cdot 10 \cdot (f_c/f_p) \cdot (D_c/D_p)^{-x} \cdot A = F$

where P is the primary production in gC/m^2/yr

while f_c and f_p are the number of size fractions occupied by the fish and the phytoplankton on the grade scale, respectively. D_c and D_p are the relative mean linear sizes (i.e., equivalent spherical diameters in μm) of the fish and the phytoplankton, respectively and A is the area of the fishery in km^2; the factor 10 is used to convert from units of carbon to dry weight (2) and from dry weight to wet weight (5); F is the annual production of adult fish taken as twice the annual catch of fish (Dickie 1972) in metric tons (wet weight) in the area (A). The equation is given in this form because it employs the most often used units for primary production, fish catch and linear dimension of the plankton. (Note that in this equation, the conversion of m^2 to km^2 is cancelled out by the conversion of grams to tonnes).

Figures for the size of the Pacific whiting fishery from the Strait of Georgia, and the mean size range of the fish caught, came from McFarlane and Beamish (1985), as well as from some recent data, kindly supplied by Dr. McFarlane of the Department of Fisheries and Oceans, Nanaimo, B.C. The weights of fish were converted to equivalent spherical diameters in the same way as for the salmon above and reported in Table 1. The area of the Strait of Georgia was taken from Harrison et al. (1983) as 6,900 km^2.

The size of the nearshore and offshore fisheries of Kaohsiung was taken from the Fisheries Year-book, 1992, Fisheries Department, Bureau of Reconstruction, Kaohsiung Municipal Government. The catch of both fisheries was averaged for the last 5 years. The nearshore fishery consisted of overnight fishermen from Kaohsiung. It was de-

fined by an offshore limit of 12 nautical miles from the coast and a linear distance along the coast of 192 km (i.e., two times the distance travelled in 12 hr by a fishing vessel at a speed of 8 knots). The offshore fishery was defined by a semicircle with a radius of 200 nautical miles centered on the city of Kaohsiung. This gives an area for this fishery of 215×10^3 km^2; however, this includes some of the area within territorial boundaries between Taiwan and the coast of China, and the coastline of the Philippines. Allowing for an exclusion zone bounded by a line equidistant between these two locations, the possible area of this fishery is 158×10^3 km^2 which is the value used in Table 1. The types of fish landed by these two fisheries were extremely diverse. A size spectrum was constructed on the basis of all species of fish reported to be over 10 per cent of the total catch, excluding very large fish, such as sharks. The principal species in this group for the nearshore fishery, excluding molluscs, were sea bream (*Sparus sarba*) and a wide assortment of fish listed as "others". The size spectrum of these fish was judged from weighed samples collected from the market place; the size range was from 4 to 10 cm with a grade scale mean of 6.34 cm. The principal species of fish in the offshore fishery were *Polynemus* spp., *Sillago* spp., *Nematolosa nasus, Coryphaena hippurus, Scomber* spp., *Saurida* spp., *Mene maculatao, Carangoides* spp., small squids, sardines, and smelt. Together these fish had a size spectrum of 4 to 16 cm with a grade scale mean at 7.12 cm.

All of the above data are entered in Table 1; Equation-1 above was then applied to each fishery to calculate the trophic efficiency exponent, x.

RESULTS AND DISCUSSION

Table 1 shows that the calculated values of the trophic efficiency exponents for two fisheries, the Gulf of Alaska salmon and the Strait of Georgia Pacific whiting, are similar (-0.735 and -0.768, respectively). Assuming a 14:1 size ratio for each step in the food chain (see Sheldon et al. 1982) this translates into a slightly higher trophic efficiency for the Gulf of Alaska of 14.3% compared with 13.2% for the Strait of Georgia whiting fishery. The ecological efficiency exponent for the offshore Kaohsiung fishery is the lowest and can again be interpreted as an average ecological efficiency for one step in the food chain of 16.2%. The highest value for this exponent is found in the nearshore Kaohsiung fishery (-0.985) which is an ecological

efficiency of only 7.4%. The reason for this much lower ecological efficiency in the nearshore Kaohsiung fishery may be two-fold. Firstly, the very high primary productivity of these waters may cause a decline in transfer efficiency, at least at the first step in the food chain (e.g., Cushing 1971, see below); and/or secondly, the anthropogenic impact of pollutants on this ecosystem (e.g., Chen et al. 1988) could cause decreased trophic efficiencies throughout the food chain.

Cushing (1971) noted that the transfer coefficient (E_T) of primary production to secondary production decreased with an increase in primary production which he attributed to superfluous feeding. His approximate relationship can be given as:

$$EQU-2 \qquad E_T = 17 - 8.5 \cdot P$$

where the transfer coefficient is per centum and P is the daily primary productivity in gC/m^2/day. Applying the estimated average primary production of 1.094 gC/m^2/day to EQU-2 for the nearshore fishery of Kaohsiung, a value for their transfer efficiency of 7.7% is obtained. This is very similar to the value obtained above of 7.4%, which came from the size spectrum data in Table 1. Thus the lower trophic efficiency of the nearshore environment can probably be explained either by superfluous feeding (i.e., a lower assimilation efficiency, Cushing 1971) or by poor trophic phasing (Parsons 1988), at least at the first step in the food chain. If this is true, then it is not necessary to invoke an explanation for any form of stress on this coastal food chain (e.g., from pollutants), other than eutrophication from a large domestic outfall situated near the city of Kaohsiung. However, in EQU-1, if there is any substantial unreported fish catch (F/2), or any significant overestimation in the area (A) of overnight fishing, it would lead to a higher trophic efficiency exponent, closer to the values obtained for the other three fisheries. Conversely, if the area is being overfished, this would also appear as a higher exponent since less of the primary production would find its way into the pelagic fishery, but more would be available to the benthic community.

The general range of values of the ecological efficiency exponent in Table 1 would seem to support the earlier suggestion by Sheldon et al. (1977) that ecological efficiency is governed by the growth rate of different trophic levels and not by a change in the standing stock. However, recent literature strongly suggests that there is also a component

in the ecological efficiency which is governed by a decrease in biomass from plankton to fish (cf. Platt and Denman 1978, Quinones and Platt 1994) at least at the lower trophic levels. In fact, the trophic efficiency exponent need not have fixed value. For example, on the basis of Fenchel's (1974) work, the value of -0.72 used by Sheldon et al. (1982) could be as high as -0.825. If, in addition to this, there are environmental reasons why trophic efficiency should decline, such as a decline in ecological efficiency with increased primary production (Cushing 1971), then the exponent being calculated in Table 1 must be regarded as having considerable potential variance between ecosystems, as has been indicated by some other reports (e.g., Sprules and Munawar 1986). This exponent is probably better thought of as a measure of "trophic phasing" efficiency (Parsons 1988). The importance of this concept lies in the fact that the smaller particles in the food chain of the pelagic environment can often grow too rapidly in proportion to their larger predators. Since smaller particles, which are not eaten, can only sink out of the water column to the benthos or deeper layers, any tendency for the food supply of the pelagic environment to outstrip the growth rate of its predators, results in poor trophic phasing — a property of marine food chains which is not seen in terrestrial environments where grasslands and trees store energy.

In conclusion, Table 1 illustrates the sensitivity of the ecological efficiency exponent to four very different environmental conditions. The data indicate that it may be possible to make approximate estimates of pelagic fish production in healthy marine ecosystems from data on primary production. This is particularly important in being able to relate changes in primary production caused by climate (e.g., global warming) to potential oceanic changes in fish catch, or, in coastal areas, to the effect of eutrophication, or other forms of pollution, on the food chain link between primary producers and fisheries.

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利用浮游植物和魚類體型分布估算不同環境之食物鏈傳遞效率

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　　本研究以浮游植物、魚類之體型分布及其生產力大小計算四種漁業之食物鏈傳遞效率，結果顯示阿拉斯加灣之鮭魚及喬治亞海峽之北太平洋鯡類漁業，其食物鏈階層間之平均生態效率分別爲14.3％及13.2％，高雄外海漁業之生態效率最高，爲16.2％，相對的高雄近海漁業之生態效率卻只有7.4％，此可能因沿岸海水優養化，降低了生態系食物鏈傳遞效率或此海域過度漁撈所致。

　　估計食物鏈傳遞效率指數之重要性在於不僅可用以偵測環境或人爲汙染對漁業之壓力，同時可利用此指數加上基礎生產力大小及基礎生產者之體型分布，估算某特定漁業之生產量。

關鍵詞：基礎生產力，體型分布，漁業。

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