



One hundred million tonnes of fish, and fisheries research¹

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Accepted 18 July 1995

Abstract

The nominal fish harvest of 100×10^6 t reported for 1993, while exceeding many early predictions of “potential yield” remains well below some other, more optimistic predictions. The key elements of a sample of prediction of marine fish potentials are reviewed, enabling identification of their shared features. One of these is the tendency for initial guesses (e.g. of the relations between optimal catches and production, of conversion efficiencies between trophic levels, or of the trophic level of harvested fish) to become legitimized with age. This has led to debates on potential yields turning into circular arguments. Obviously, a way out of this is also proposed.

Keywords: Potential yields; Global catch; Gulland’s equation; Food web; Transfer efficiency

1. Introduction

The world’s fisheries harvest for 1993, the last year for which an FAO estimate is available, has finally reached 100×10^6 t year⁻¹; *Fisheries Research* has reached the proud age of 25, and I will soon reach 50, widely accepted as the minimum age for pontificating.

Such confluence of multiples often serves as an excuse for some review, and an obvious topic, given the first number above, is the minor industry which, in the last four decades, has generated successive estimates of potential yield from the world oceans. As we shall see, this will confront us with the best and worst of fisheries research — bold attempts to synthesize the consensual knowledge of the time, succeeded by spurious “confirmations” of the explicit or implicit guesses involved in these syntheses.

I shall illustrate this through a series of case studies, documented mainly through salient quotes, i.e. those parts of the text that presented the assumptions and numbers (and their

¹ Invited paper for the 25th Anniversary issue of *Fisheries Research*; ICLARM Contribution No. 1153.

Table 1

Some estimates of the potential fisheries of the oceans (modified from Schaefer and Alverson, 1968 with additions)

Author(s)	Year	Estimate ($t \cdot 10^6 \text{ year}^{-1}$)	Method(s) ^a	Remarks
Thompson	1951	22	A	–
FAO	1953	55	A, B	–
Finn	1960/1961	50–60	A, B	–
Graham and Edwards	1962	55	B	Bony fish only, i.e. 2/3 of available nekton
Graham and Edwards	1962	115	C	
Mesek	1962	55	A	To be reached by 1970
Pike and Spilhaus	1962	180–1400	C	–
Schaefer	1965	200	C	See text
Chapman	1965	2000	C	–
Ricker	1969	150–160	C	Comprehensive review
Ryther	1969	100	C	See text
Gulland	1970	100	A, B	Conventional species only
Gulland	1970	260–350	A, B, C	Including non-conventional spp.
Idyll	1978	400–700	None	See text
Moiseev	1994	120–150	D	See text

^aA, extrapolation of catch trends; B, extrapolation from known area to the global ocean; C, extrapolations from primary production and food chains; D, biomass \times P/B \times factor (as in Moiseev, 1994).

sources, if any) crucial to each case study. I have made no attempt to document all potential yield estimates presented so far (see Table 1 for a larger sample). Rather, only selected cases are provided, for which, however, I include all the evidence needed to reconstruct the estimate(s) of world ocean potential they contain. For simplicity's sake, I will refer only to marine fisheries, i.e. omit freshwater fisheries (included in FAO's estimate of 100×10^6 t for 1993), aquaculture (i.e. the farming of fish and other aquatic organisms, also included in FAO's 100×10^6 t) and the harvesting of marine mammals (whose "potential" is a political, not a biological issue).

Also, I will not discuss the earlier work of Moiseev, 1969, whose comprehensive study avoided most of the pitfalls identified below but whose English translation of 1971 did not influence the tradition that had then emerged.

2. Early notions of the potential catch of the ocean

Given the absence of direct experience analogous to that gained in agriculture and fish pond culture, whose potentials and limitations were fairly known to ancient authors, dealing with early notions of marine catch potential is not very illustrative. Thus, only two of these notions shall be briefly mentioned here.

The first of these is that the ancient Greek fishers appear to have been aware that factors other than fishing effort did limit their catch. Thus, Aristotle, in his *Historia Animalium* reports that fishers knew that if "auxids" (small tuna) and "pelamyds" (middle sized tuna) were abundant in a given year, "full grown tuna" would also be abundant in the following years, and conversely: an early understanding of recruitment variability, and of its consequences for catches (D'Arcy Thompson, 1910).

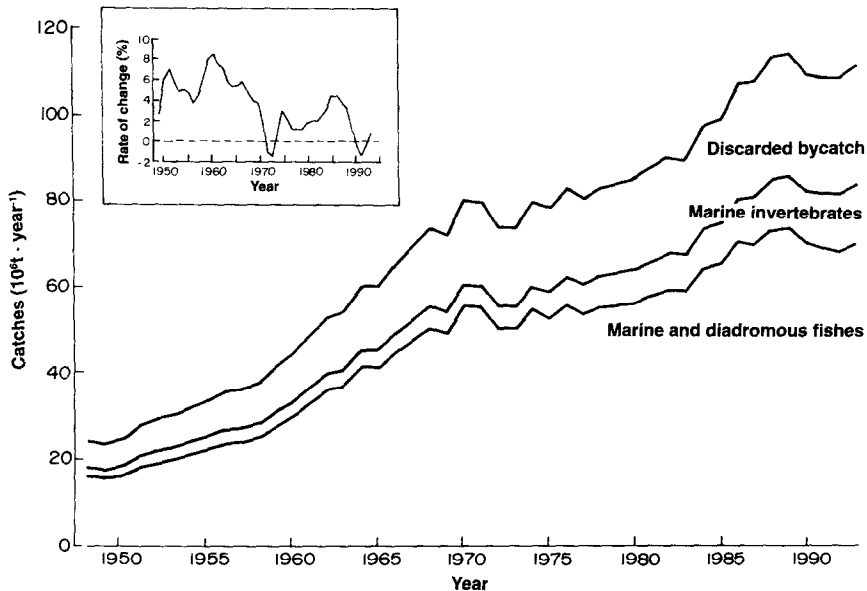


Fig. 1. Global marine catches, 1948–1993. To account for discarded bycatch, the estimate $27 \times 10^6 \text{ t year}^{-1}$ of Alverson et al., 1994 was applied to 1992, and prorated to the total catch of all other years. This maintains the structure of the time series, which clearly reflects the collapse of the Peruvian anchoveta in the early 1970s, and its increase in the last 2–3 years, which masks the decline of other major groups. The insert shows the percentage rate of change of the series, smoothed over three years (adapted from FAO yearbooks).

The second early notion to be mentioned here — and I am aware I make a jump of over two thousand years, skipping important medieval and other developments described e.g. in Cushing, 1982 — is the belief held by many authors of the last century, that the fish resources of the oceans were essentially inexhaustible. T. Huxley, a friend of Charles Darwin, and F. Buckland, one of his detractors, are often cited in this context, but I shall quote here Charles Lyell, Darwin's mentor, and an intellectual giant of the first half of the 19th century. Lyell, 1830 believed that ‘even now, the waters of lakes, seas and the great ocean, which teem with life, may be said to have no relation to the human race — to be portions of the terrestrial system of which men has never taken, nor can take possession’.

Fisheries science emerged well after this gloriously wrong prediction was made (Smith, 1994); yet one could use, as a measure of our scientific progress, the degree to which we can assess the limits of the world's fisheries potential, and hence refute Lyell.

3. The study of Graham and Edwards (1962)

At an FAO conference on ‘Fish in Nutrition’ held in Washington, DC in 1961, at a time when the world's marine catch was about $35 \times 10^6 \text{ t}$ (Fig. 1), Graham and Edwards, 1962 presented two global estimates of world fisheries potentials.

The first of these was based on the following steps:

(1) “The harvest levels of demersal species, from 7.7 to 12.7 lb. per acre are surprisingly similar.” (This resulted from comparisons among different parts of the North Atlantic and adjacent seas.)

(2) “The pelagic harvest rates, on the other hand, vary extremely, from 0.2 to 54.2 lb. per acre”.

(3) “For purposes of computing the possible world harvest from all Continental Shelves, we can use the value for North Atlantic banks. Let us pick 20 lb. per acre as a conservative average figure” (i.e. 2.2 t km^{-2}).

(4) “Over the entire globe there are approximately 6×10^9 acres of potentially productive Continental Shelf” (i.e. $2.4 \times 10^6 \text{ km}^2$); hence “on this basis, the total Continental Shelf yield would be 120 billion lb. or 55 million metric tons per year”.

Graham and Edwards’ second estimate was based “on an independent, more theoretical technique” adapted from Kesteven and Holt, 1955, as follows:

(5) Steeman-Nielsen (1960) estimated the world’s primary production (PP) as a ratio of 37:1 for the carbon to wet weight conversion (Sverdrup et al., 1946) leads to a global PP of about $50 \times 10^{10} \text{ t wet weight}$.

(7) Herbivorous zooplankton fully exploit the PP, and 20% of their food intake is passed on to the next trophic level (“primary carnivores”).

(8) The primary and secondary carnivores have a conversion efficiency of 10%, leading to an annual global production of 10^{10} primary and 10^9 t secondary carnivores.

(9) About 30% of “theoretical energy transfer” are “sidetracked” (e.g. sedimented, leading e.g. to “petroleum deposits”); this may reduce the efficiencies in (7) and (8) to 14, 7 and 7% respectively and hence “our estimated annual production of secondary carnivores is approximately 343 million metric tons”.

(10) “Included in this figure, in addition to the marine fish in which we are principally interested are many other marine animals such as squids, whale or sharks which we conservatively estimate make up one-third of the consuming biomass at this and higher consumer level. All things considered, then perhaps 230 million metric tons of marine bony fishes are produced on an annual basis”.

(11) “Properly harvested, it is reasonable to suggest that resources of this nature may yield 50 per cent by weight, at last, of the net annual production”.

(12) “We estimate finally, therefore, that perhaps as much as 115 million metric tons of marine fishes may be available for harvest each year. A significant part of this resource is thinly scattered [and] our fishery technology will have to be greatly improved before a harvest of this magnitude is possible or feasible”.

Of Graham and Edwards’ estimates, the first is based on data (steps 1–4), although marred by the assumptions that the north Atlantic was then fully exploited, and globally representative. The line of reasoning leading to the second estimate, while also starting with data (steps 5 and 6), depends entirely on the guesses in steps 7–11, of which 11 is the most interesting: we shall encounter it again, if under a different guise.

4. The study of Schaefer, 1965

Schaefer, 1965 identified three approaches for estimating potential yields: (a) “by extrapolation of recent trends (a dangerous business for looking more than a few years into the

future)''; (b) ''by considering our knowledge of unused harvestable resources''; and (c) ''by calculations based on food chain dynamics''.

He then presented a fine review of earlier attempts to estimate marine potential yields, and concluded by presenting his estimate, which relied entirely on (c). His line of reasoning was as follows:

(13) Slobodkin, 1961 based on laboratory experiments, estimated a transfer of efficiency of about 10% between trophic levels;

(14) ''Effective ecological efficiency, due to [...] recycling, may be higher than the 10% estimate; 15% would not seem an unreasonable guess and 20% should be possible''.

(15) ''Currently, 37% of the marine fishing harvest consists of [fish which] feed on a mixture of phytoplankton and zooplankton. So, perhaps this harvest corresponds to about 1 1/2 steps above the phyto. ''The remainder of the harvest is from levels a step or two higher. We are, I think, very conservative if we assume the harvest is all taken at step 3''.

(16) Given a PP of 19×10^9 t carbon (from Pike and Spilhaus, 1962, and ''based on very inadequate data'') leads, with a 10% efficiency between trophic levels to a potential of 190×10^6 t; with 15%, this leads to 640×10^6 t per year.

(17) Moreover, ''if we assume that half of the potential might be taken at step 2 and half of step 3, which is more nearly realistic'', the available potentials become 1 080 and $2\,420 \times 10^6$ t year⁻¹, respectively.

(18) ''Only a part of this can be realized, because of economic inability to harvest some of the components that are diffusely distributed, and because other predators than man take a share of the potential harvest''.

(19) ''A minimum estimate of $200 \cdot 10^6$ tons would appear to me reasonable and probably conservative''.

(20) ''Calculations of this sort by Graham and Edwards provide somewhat similar results [...]. If one includes the other organisms, discarded in Graham and Edward's calculation, the corresponding estimate of available harvest is 171×10^6 tons''.

Schaefer's line of reasoning starts with data (step 13); all subsequent steps are based on guesses; the last step then shows that the result is similar to that obtained in an earlier study, itself based on a series of guesses.

5. Ryther, 1969 and his critics

Ryther, 1969 appears to have been among the first to use geographic strata or ''provinces'' for estimating world fisheries potential, viz: (i) the open seas (326×10^6 km²) with a PP of 50 g C m⁻² year⁻¹ and a food chain length of 5 steps (PP; herbivores; 1st; 2nd; and 3rd stage carnivores, i.e. tuna); (ii) coastal waters (i.e. areas down to 100 fathoms, or 180 m, slightly less than the 200 m limit commonly used to define continental shelves) and ''off-shore regions of comparably high productivity'', with a mean PP of 100 g C m⁻² year⁻¹, a surface area of 36×10^6 km², and a food chain length of 3 steps; (iii) upwelling system, with an approximate area of 3.6×10^5 km², a mean PP of 300 g C m⁻² year⁻¹ of a food chain length of 2 1/2 steps (PP; herbivorous zooplankton; and fish feeding on both phyto- and zooplankton).

The transfer efficiencies required for each province were guessed, then the conclusions drawn, viz:

(21) “Slododkin (1961) concludes that an ecological efficiency of about 10% is possible and Schaeffer (sic) feels that the figure may be as high as 20%. 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”.

(22) “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 errors, it should not be considered significantly different from Schaeffer’s figure of 200 million tons”.

(23) “Production however is not equivalent to potential harvest. In the first place, man must share the production with other top level carnivores [...]. In addition, man must take care to leave a large enough fraction of the annual production to permit utilization of the resource at something close to its maximum sustainable yield [...]. When these various factors are taken into account, it seems unlikely that the potential sustained yield of fish to man is appreciably greater than 100 million tons” [Note the implied ratio of about 2:1 between production and catches, explicit in Graham and Edwards.]

Alverson et al. (1970) took issue with almost all of Ryther’s numbers, assumptions and illustrative examples (not documented here). Notably, they suggested that “his selection, for his calculations, of relatively high trophic levels from the coastal and oceanic provinces is questionable”. They granted that Ryther “may be right but for the wrong reason. If the world catch of sea fishes levels off, 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”.

Interestingly, two of the four alternatives to “inadequacy of unexploited resources” (overfishing and jurisdiction problems) are directly related to the deployment (at least locally) of excessive effort relative to the size of a (local) fish resource. The third alternative (“climatic cycles”) anticipates the collapse of the Peruvian anchoveta fishery in the early 1970s (Fig. 1), which had been the largest in the world, and is now widely recognized to have succumbed to an El Niño event combined with excessive effort (see contributions in Pauly et al., 1989). (One interesting side aspect of the change in wind patterns predicted to occur under global warming is that the habitat of anchoveta should increase (Bakun, 1990). The recent increase of their catches, which led to the recent increase of global catches shown in Fig. 1, may be in line with this.)

Alverson et al., 1970, in their critique of Ryther, 1969 may also have been “right for the wrong reasons”: they questioned the high trophic levels he used, but not his transfer efficiencies, for which he presented even less justification than for the trophic levels (though a subsequent study shall “confirm” them, see below).

Also, one must ask what it is that Ryther, 1969 was “right about”. Alverson et al. mention a then ongoing major FAO study (which led to the report edited by Gulland, 1970), and which they implied would lead to more reliable estimates than Ryther’s approach. As we shall see, that study did lead to a potential yield (of conventional species) close to Ryther’s estimate and thus, he was “right” (but again, for the wrong reason).

6. Gulland's review of 1970

The lucid review of Gulland (1970) discusses, as did Schaefer, 1965, three approaches for global potential estimate, i.e.: (a) extrapolation of catch trends; (b) extrapolation from known areas to the global ocean; and (c) extrapolations from primary production and transfer efficiencies.

[As may be noted, item (b) differs conceptually from Schaefer's second approach, while (a) and (c) overlap with his first and last approach, respectively.]

Gulland then went on to discuss the pitfalls of these methods, and likely errors associated with each. His subsequent estimate of global potential yield differs from those listed above in that the logic of its derivation cannot be summarized by a brief sequence of statements. Rather, his key estimate i.e. the global potential for "conventional" species, of 100×10^6 t year⁻¹, results from the addition of a large number of largely independent, area-specific estimates, obtained (by various authors commissioned by FAO) through various combinations of (a), (b) and (c). This approach, similar to that of Moiseev, 1969, leads to estimates that are far more robust than the estimates obtained by multiplication of a few guessed numbers (see below).

To account for "unconventional" species, Gulland, 1970 guessed potentials of 10–100 × 10⁶ t for cephalopods, "100+" × 10⁶ t for "lanternfish, etc.", and "50+" × 10⁶ t for euphausiids in Antarctica.

One important feature of the FAO review edited by Gulland, and widely circulated in book form (Gulland, 1971) is that it provided, in its Preface, the derivation of the famous "Gulland equation" (The originators of this equation appear to be Alverson and Pereyra (1969), who present the same logic as presented below, but who are not formally cited in Gulland's Preface.) for estimation of potential yield, viz

$$\text{Potential yield} = 0.5 \cdot M \cdot B_o \quad (1)$$

where M is the natural mortality of the stock in question, and B_o its unexploited biomass.

This was based on two sets of arguments:

(24) The surplus production model of Schaefer, 1954 implies that unexploited biomass is halved when maximum sustainable yield (MSY) is achieved; thus, if $F_{\text{MSY}} \approx M$, then Eqn. (1) applies.

(25) Yield-per-recruit (Beverton and Holt, 1964) is optimized for values of mean lengths at first capture (L_c) ranging from 40 to 70% of asymptotic length (L_∞), when $F \approx M$.

Given that production/biomass ratio (P/B) is equivalent to total mortality ($Z = F + M$) for standard representations of growth and mortality (Allen, 1971), Gulland's equation implies that MSY represents 50% of biological production — precisely the assumption of Graham and Edwards, 1962 (see above).

Many subsequent authors built on this assumption (see e.g. Dickie, 1972, Parsons and Chen, 1994), but dedicated studies (Francis, 1974, Beddington and Cooke, 1983, Kirkwood et al., 1994), (Christensen, 1995) shows it to be untenable: the fishing mortality which maximizes sustainable yield is for most single or multispecies fish stocks much smaller than M , i.e. $F_{\text{MSY}} \approx 0.2 - 0.5 \times M$. The implications for potential yield estimates that assume $F_{\text{MSY}} \approx M$ are obvious. Also, as noted by L. Alverson (personal communication, 1995) we do not know that M at B_o is equal to M at $B_o/2$.

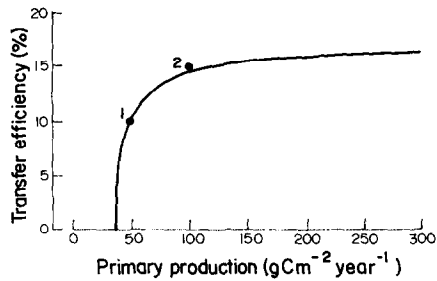


Fig. 2. Reproduction of Fig. 7 in Iverson, 1990, showing “C transfer efficiency as a function of total phytoplankton production [...] Estimates of transfer efficiency for (1) oceanic and (2) coastal non-upwelling environments were assumed by Ryther, 1969”. Note that this neat “confirmation” fails, however, to accommodate Ryther’s 20% guess for upwelling systems (see also text and Fig. 4).

7. Idyll’s view of 1978

Based on a summary of the above cited contributions, Idyll, 1978 concluded that:

(26) “[T]he biological evidence is strong that the potential for familiar kind of seafood is 100 to 120 millions tons”.

(27) However, impressed by Gulland’s estimates for unconventional species, he concluded that “it does not seem unreasonable to suppose that a total of all species of 400 millions tons could be caught, and it might be as large as 700 million tons”.

8. The study of Iverson, 1990

Iverson, 1990 did not set out to estimate the global potential of the ocean, but perhaps more ambitiously, to identify the factors that “control [...] marine fish production”.

His methodology and data sets are rather opaque and need not concern us here except insofar as he deals with trophic levels (TL) and the transfer efficiencies (TE) between these, which he relates through the following steps:

$$(28) \text{ Fish production} = PP \cdot TE^{TL} \quad (2)$$

where TL is “set equal to a non-integer value to represent fish production as the average of production on several trophic levels (Ryther, 1969)”.

(29) “The results of an analysis of N stable isotope data (Fry, 1988) suggest that the average trophic status of the species providing most of Georges Bank fish production can be characterized by $[TL] = 2.5$. A similar value was assumed for food chains on northeast North American coastal environments [...]; catches of the Baltic sea environments include herring, sprat and cod, which are assumed to be characterized by an average value for $[TL]$ similar to the Georges Bank value”.

These guesses, plus a few more for mesopelagic fishes, and a few iterations of Eqn. (2) led to the curve in Fig. 2, which conveniently replicates the transfer efficiencies assumed by Ryther, 1969 and before him, by Schaefer, 1965.

9. Moiseev returns

In a brief communication presented in 1992 at the 1st World Fisheries Congress, Moiseev, 1994 included a table whose ten elements add up to a global biomass nekton of $6-7 \cdot 10^9$ t, and a production of $4-5 \cdot 10^9$ t year⁻¹. Further, he suggested that:

(30) “The biomass of large fish and other organisms which form the basis of conventional present day fisheries is estimated at about 1.5 billions tonnes”. Using a P/B ratio of 0.4 year⁻¹, he estimates for these a production 600×10^6 t year. He then concludes that “the possible yield of conventional fishing may reach 120–150 million tonnes (20–25%) of the production; that of organisms at lower trophic levels may be many time more”.

This implies $F_{MSY} \ll M$, thus confirming Moiseev’s independence, alluded to above, from the tradition embodied in the cases reviewed above.

10. Discussion

Since 1989, V. Christensen and D. Pauly have collaborated on the further development of the ECOPATH approach and software proposed by J. Polovina and colleagues (Polovina, 1984a, Polovina, 1984b, Polovina, 1985, Polovina and Ow, 1983, Atkinson and Grigg, 1984) for routine construction and balancing of trophic models of ecosystems.

The resulting product, ECOPATH II, has been well documented (Christensen and Pauly, 1992a, Christensen and Pauly, 1992b) and widely applied, by them (see e.g. Pauly and Christensen, 1993) and many others (see e.g. contributions in Christensen and Pauly, 1993).

These applications are constructed so that the ecosystem components are first arranged in a number of functional groups. For each of these groups the production, consumption, and diet is quantified, and a possible model with a set of mutually compatible trophic fluxes is constructed by the program (using a least-square approach in the newest version of ECOPATH II). An example of such a model is given in Fig. 3. The formalized approach has allowed a number of generalizations to emerge that are pertinent to the estimation of global potentials. Fig. 4 is an example of this; it suggests that mean TE values of 15% and beyond, used by several of the above cited authors would not have been found, had actual food webs been studied, rather than hypothetical food chains. Furthermore, for reasons not discussed here (but see Jarre-Teichmann and Christensen, 1995) upwelling systems tend to have much lower than average TE and not a mean TE of 20% as assumed e.g. in Ryther, 1969.

Another generalization is that predation by fish removes from most exploited stocks far more biomass than even intense fisheries, confirming Moiseev, 1994 that $F_{opt} \ll M$ (see e.g. Pauly and Christensen, 1993).

A further generalization is that, due to the non-linearity of the relationships between trophic levels and trophic fluxes, use of “mean trophic level” for estimating fluxes in multispecies fisheries leads to a strong bias, which can be quantified using the data in Table 1 of Pauly and Christensen, 1995.

That table, inspired by Vitousek et al., 1986, contains estimates of the primary production required (PPR) to sustain the global catches of 39 different groups of fish (*i*), each calculated using the inverse of Eqn. (2) viz

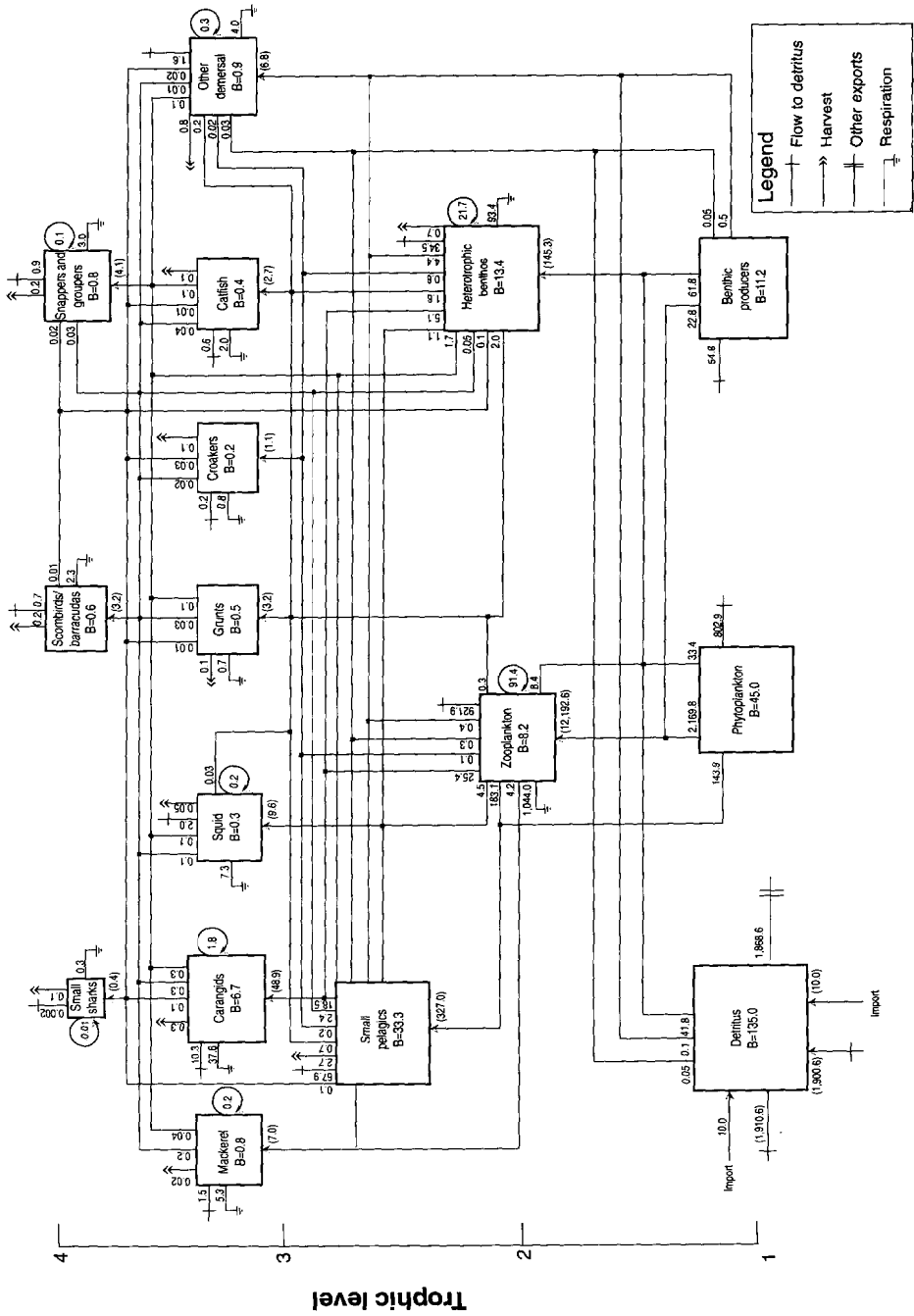


Fig. 3. Trophic flux model of the northeastern Venezuelan shelf, constructed using the ECOPATH II approach and software (from Mendoza, 1993). Note the reticulated nature of the major fluxes, invalidating the notion of linear food chains, and leading, for the various consumers (boxes), to (fractional) trophic levels that are estimated, i.e. represent model output, rather than assumed input.

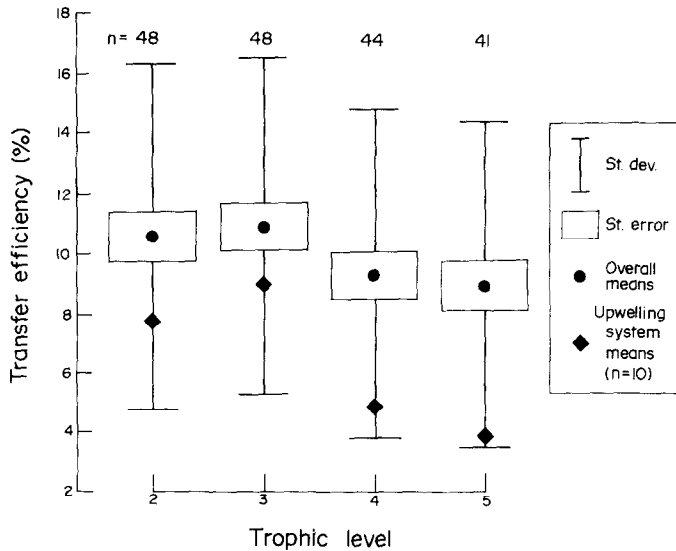


Fig. 4. Trophic transfer efficiency (TE , %) in 48 models of trophic flows in aquatic ecosystems by trophic level; based on the same sources as Figure 2 in Pauly and Christensen, 1995. Note the overall mean of about 10%, and the low means for upwelling systems, contradicting earlier assumptions.

$$PPR_i = \text{catches}_i (1/TE)^{(TL_i-1)} \quad (3)$$

with a mean value of $TE = 0.10$ (see Fig. 4), and TL_i values derived from 48 trophic models as used in Fig. 3.

The sum of these estimates is 2.84×10^9 t C year⁻¹. The mean TL of these 39 groups, weighted by their catch is 3.10. This, applied to the sum of the catches leads via Eqn. (3), to a PPR estimate of $PPR = 1.33 \times 10^9$ t year⁻¹, or 47% of the previous estimate, obtained with disaggregated data.

Thus, using mean TL values, as in most publications previously reviewed above, completely distorts the relationships between PP and catches or potential yields.

Using a large number of groups when estimating PPR not only has the effect of reducing the bias due to non-linearity, but also leads to robust estimates, wherein an overestimate of one or the other parameter is compensated for, at least in part, by underestimates of other parameters.

This effect, leading to what may be called ‘‘a large Fermi solution’’ (Von Baeyer, 1993), and obviously an implication of the Central Limit Theorem (Sokal and Rohlf, 1995), has been used by few of the above-cited authors. Only in the FAO study led by J.A. Gulland, and in Moiseev, 1969 was the world ocean and its resources broken into enough strata for this effect to occur.

One side effect of such stratification is obviously that it allows the identification of problematic strata. Thus, the information that the PPR required to sustain the world’s fisheries is 8% of the world’s primary production is not as telling as the information that PPR is very low in open ocean waters, 2%, and very high on continental shelves, 25–35% (Pauly and Christensen, 1995).

The studies which led to these considerations are continuing, and now based on a version of ECOPATH II which includes a Monte Carlo simulation routine, allowing explicit consideration of uncertainty in the inputs, and selection of “best” solutions using a least squares criterion (Christensen and Pauly, 1995). We hope they will allow overcoming the tradition which led to some of the circular arguments presented above.

Acknowledgements

I take this opportunity to thank my partner Villy Christensen for many years of fruitful collaboration, and for his comments on this MS: once again, he spotted errors I would have hated to see printed. I also thank Lee Alverson for comments, made particularly valuable by his having been a key actor in the performance reviewed here.

References

- Allen, K.R., 1971. Relation between production and biomass. *J. Fish. Res. Board Can.*, 28: 1573–1581.
- Alverson, D.L. and Pereyra, W.T., 1969. Demersal fish exploration in the Northeastern Pacific Ocean — an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecast. *J. Fish. Res. Board Can.*, 26: 1185–2001.
- Alverson, D.L., Longhurst, A.R. and Gulland, J.A., 1970. How much food from the sea? *Science (Wash.)*, 168: 503–505.
- Alverson, D.L., Freeberg, M.H., Murawski, S.A. and Pope, J.G., 1994. A global assessment of fisheries bycatch and discards. *FAO Fish. Tech. Pap.* (339), 233 pp.
- Atkinson, M.J. and Grigg, R.W., 1984. Model of a coral reef ecosystem. II. Gross and net primary production at French Frigate Shoals, Hawaii. *Coral Reefs*, 3: 13–22.
- Bakun, A., 1990. Global climate change and intensification of coastal ocean upwelling. *Science (Wash.)*, 247: 198–201.
- Beddington, J.R. and Cooke, J.G., 1983. The potential yield of fish stocks. *FAO Fish. Tech. Pap.* (242), 47 pp.
- Beverton, R.H.J. and Holt, S.J., 1964. Tables of yield functions for fishing assessment. *FAO Fish Tech. Pap.* (38), 49 pp.
- Chapman, W.M., 1965. Potential resources of the oceans. Van Camp Sea Food Co., Port of Long Beach, CA, 43 pp.
- Christensen, V., 1995. Managing fisheries involving top predator and prey components, submitted.
- Christensen, V. and Pauly, D., 1992a. ECOPATH II — a system for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Modelling*, 61: 169–185.
- Christensen, V. and Pauly, D., 1992b. A guide to the ECOPATH software system (version 2.1). *ICLARM Software 6*, 72 pp.
- Christensen, V. and Pauly, D., 1993. Trophic models of aquatic ecosystems. *ICLARM Conf. Proc.* 26, 390 pp.
- Christensen, V. and Pauly, D., 1995. Fish production, catches and the carrying capacity of the world ocean. *Naga, the ICLARM Quarterly*, 18(3): 34–40.
- Cushing, D.H., 1982. *Climate and Fisheries*. Academic Press, London, 373 pp.
- D’Arcy Thompson, W., 1910. The work of Aristotle. In: J.A. Smith and W.D. Ross (Editors), *Historia Animalium* Vol. 14. Clarendon Press, Oxford, 633 pp.
- Dickie, L.M., 1972. Food chains and fish production. In: *Symposium on Environmental Conditions in the North-west Atlantic, 1960–1969*. ICNAF Special Publications No. 8, pp. 201–221.
- FAO, 1953. Improving the fisheries contribution to world food supplies. *FAO Fish. Bull.*, 6(5): 159–192.
- Finn, D.B., 1960. Fish: the great potential food supply. *World Food Problems* No. 3. FAO, Rome, 49 pp.
- Finn, D.B., 1961. Freedom from hunger. *Fis. News Int.*, 1(1), October.

- Francis, R.C., 1974. Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *J. Fish. Res. Board Can.*, 31: 1539–1542.
- Fry, B., 1988. Food web structure on Georges Bank from stable C, N and S isotopic compositions. *Limnol. Oceanogr.*, 33: 1182–1189.
- Graham, H.W. and Edwards, R.L., 1962. The world biomass of marine fishes. In: E. Heen and R. Kreuzer (Editors), *Fish in Nutrition*. Fishing News (Books), London, p. 3–8.
- Gulland, J.A., 1970. Summary. In: J.A. Gulland (compiler and editor), *The Fish Resources of the Ocean*. FAO Fish. Tech. Pap. 97.
- Gulland, J.A., 1971. *The Fish Resources of the Ocean*. Fishing News (Books), West Byfleet.
- Idyll, C.P., 1978. *The sea against hunger*. Thomas U. Crowell Company, New York, 222 pp.
- Iverson, R.L., 1990. Control of marine fish production. *Limn. Oceanogr.*, 35: 1593–1604.
- Jarre-Teichmann, A. and Christensen V., 1995. Trophic flows in upwelling ecosystems: temporal and spatial comparisons. *ICLARM Studies and Reviews* 24, in press.
- Kesteven, G.K. and Holt, S.J., 1955. A note on the Fisheries Resources of the North West Atlantic. *FAO Fisheries Papers No. 7*: 1–11.
- Kirkwood, G.P., Beddington J.R. and Rowwouw, J.A., 1994. Harvesting species of different lifespans. In: P.J. Edwards, R.M. May and N.R. Webb (Editors), *Large Scale Ecology and Conservation Biology*. 35th Symposium of the British Ecological Society. Blackwell Scientific, Oxford, pp. 199–227.
- Lyell, C., 1830. *Principles of Geology*. J. Murray, London, Vol. 1.
- Mendoza, J.J., 1993. A preliminary biomass budget for the northeastern Venezuela shelf ecosystem. In: V. Christensen and D. Pauly (Editors), *Trophic Models of Aquatic Ecosystems*. ICLARM Conf. Proc. 26.
- Meseck, G., 1962. Importance of fishery production and utilization in the food economy. In: E. Heen and R. Kreuzer (Editors), *Fish in Nutrition*. Fishing News (Books), London, pp. 23–38.
- Moiseev, P.A., 1969. *The Living Resources of the World Ocean Pishchevaia promyshlannost*, Moskva, 338 pp. (Translated edition 1971 by Israel Program for Scientific Translation, Jerusalem, 334 pp.)
- Moiseev, P.A., 1994. Present fish productivity and bioproduction potential of the world aquatic habitats. In: C.W. Voigtlander (Editor), *The State of the World's Fisheries Resources*. Proceedings of the World Fisheries Congress. Plenary Sessions. Oxford and IBH, New Dehli, pp. 70–75.
- Parsons, T.D. and Chen, Y.L.L., 1994. Estimates of trophic efficiency, based on the size distribution of phytoplankton and fish in different environments. *Zoological Studies*, 33(4): 296–301.
- Pauly, D., Muck, P., Tsukayama, I. and Mendo, J., (Editors), 1989. *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conf. Proc., 18, pp. 438.
- Pauly, D. and Christensen, V., 1993. Stratified models of large marine ecosystems: a general approach and an application to the South China sea. In: K. Sherman, L.M. Alexander and B.D. Gold (Editors), *Large Marine Ecosystem: Stress, Mitigation and Sustainability*. AAAS Press, Washington, DC, pp. 148–174.
- Pauly, D. and Christensen, V., 1995. Primary production required to sustain global fisheries. *Nature*, 374: 255–257.
- Pike, S.T. and Spilhaus, A., 1962. Marine resources. In: Report to the Committee on Natural Resources of the National Academy of Sciences — National Research Council. NAS/NRC Publ. 100-E, p. 1–8.
- Polovina, J.J., 1984a. An overview of the ECOPATH model. *Fishbyte*, 2(2): 5–7.
- Polovina, J.J., 1984b. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, 3: 1–11.
- Polovina, J.J., 1985. An approach to estimating an ecosystem box model. *U.S. Fish. Bull.*, 83: 457–460.
- Polovina, J.J. and Ow, O.W., 1983. ECOPATH: a user's manual and program listings. National Marine Fisheries Service, NOAA, Honolulu, Adm. Rep. H-83-23, 46 pp.
- Ricker, W.E., 1969. Food from the sea. In: *Resources and Man, the report of the Committee on Resources and Man to the U.S. National Academy of Sciences*. W.H. Freeman, San Francisco, CA.
- Ryther, J., 1969. Photosynthesis and fish production in the sea. *Science (Wash.)*, 166: 72–76.
- Schaefer, M.B., 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Bull. Inter. Amer. Trop. Tuna Comm.*, 1(2): 26–56.
- Schaefer, M.B., 1965. The potential harvest of the sea. *Trans. Amer. Fish. Soc.*, 94: 123–128.
- Schaefer, M.B. and Alverson, D.L., 1968. World Fish potentials. *Univ. Wash. Publ. Fish.*, 4: 81–85.
- Slobodkin, L.B., 1961. *Growth and regulation of animal populations*. Holt, Rinehart and Winston, New York, 184 pp.

- Smith, T.D., 1994. *Scaling fisheries: the science of measuring the effects of fishing, 1855–1955*. Cambridge University Press, Cambridge, 392 pp.
- Sokal, R.R. and Rohlf, F.J., 1995. *Biometry: Third Edition*. W.H. Freeman, New York, 887 pp.
- Steeman-Nielsen, E., 1960. Productivity of the Ocean. *Ann. Rev. Plant. Physiol.*, 11: 341–362.
- Sverdrup, H.U., Johnson M.W. and Fleming, R.H., 1946. *The Oceans, their physics, chemistry, and general biology*. Prentice-Hall, New York, 1087 pp.
- Thompson, H., 1951. Latent fisheries resources and means for their development. In: *Proc. U.N. Science Conference on Conservation and Utilization of Resources*, 7: 28–38.
- Vitousek, P.M., Ehrlich, P.R., Ehrlich A.H. and Matson, P.A., 1986. Human appropriation of the products of photosynthesis. *Bioscience*, 36: 368–373.
- Von Baeyer, H.C., 1993. *The Fermi solution: Essays on Science*. Random House, New York, 172 pp.