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Primary production required to sustain global fisheries

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THE mean of reported annual world fisheries catches for 1988–1991 (94.3 million t) was split into 39 species groups, to which fractional trophic levels, ranging from 1.0 (edible algae) to 4.2 (tunas), were assigned, based on 48 published trophic models, providing a global coverage of six major aquatic ecosystem types. The primary production required to sustain each group of species was then computed based on a mean energy transfer efficiency between trophic levels of 10%, a value that was re-estimated rather than assumed. The primary production required to sustain the reported catches, plus 27 million t of discarded bycatch, amounted to 8.0% of global aquatic primary production, nearly four times the previous estimate. By ecosystem type, the requirements were only 2% for open ocean systems, but ranged from 24 to 35% in fresh water, upwelling and shelf systems, justifying current concerns for sustainability and biodiversity.

Global primary productivity generates annually about 224×10^9 t dry weight of biomass. Of this, 59% is produced in terrestrial ecosystems, the rest in aquatic systems[1]. Of the terrestrial primary production, 35–40% is presently used by humans, directly (for example, as food or fibre), indirectly (for example, as feed for animals) or foregone (through, for example, urban sprawl)[1]. This was estimated by adding the primary production required (PPR) by various production systems (such as cultivated and grazing lands) or by various subsectors (such as timber or fibre production), thus allowing errors in the independent subtotals to cancel out partly.

The PPR to sustain the world's catches of 75 million t in the early 1980s was also estimated in the same study, based on the key assumption that the 'average fish' feeds two trophic levels above the primary producers. This suggested that 2.2% of the world's aquatic primary production was required to sustain the fisheries, and thus led to the conclusion that 'human influence on the lowest trophic levels in the ocean (outside severely polluted areas) is minimal, and human exploitation of marine resources therefore seems insufficient by itself to alter on a large scale any but the target populations and those of other species interacting closely with target species'[1].

This work is an attempt to obtain a more accurate estimate of the PPR to sustain the world fisheries catches (including discarded 'bycatch'), based on the same approach as used above to estimate terrestrial PPR, wherein independent estimates are obtained on a commodity group and system basis, then added up to yield a robust estimate of the total.

Our approach, illustrated in Fig. 1, uses only flows of matter (catches and food consumption of fishes and their prey) and does not require estimation of biomasses, which have proved hard to estimate reliably on a global basis[2].

Recent world fisheries statistics, covering a short period (1988–1991) without major changes in catch composition and reported by the UN Food and Agriculture Organization (FAO)[3], were split into 39 commodity groups, by ecosystem types. The PPR was then estimated by group, and ecosystem type, based on an estimate of 10% mean transfer efficiency between trophic levels (Fig. 2), and the mean trophic levels of the commodity groups (Table 1). This led to group-specific estimates of PPR, presented here by ecosystem type, after accounting for the 27 million t of discarded bycatch recently estimated, based on thorough review of worldwide discarding practices[4] (Table 2).

The results differ markedly from those of the previous study based on an 'average fish': we estimate that 8.0% of the world's aquatic primary production is required to sustain the fisheries, nearly four times the earlier estimate. The difference is due to our use of higher fisheries catches, our consideration of discards, and the fact that we used dissagregated data, to account for the non-linearity of the relationship between PPR and trophic levels.

Although our 8% still may be a moderate figure compared to 35–40% for the terrestrial systems, the prospects for increases are dim. The bulk of aquatic productivity (75%) occurs in the open ocean (gyre) systems, by virtue of their vast extent. Only 1.8% of this productivity is used, but as little as 20 to 25% of the overall zooplankton biomass may be available for the higher trophic levels[5], dominated by top predators (notably yellowfin and skipjack tuna), which must roam desert-like ocean expanses to find scattered food patches.

The estimated PPR for the coastal and coral reef systems is 8.3%. This relatively low value is due to (1) a high level of productivity (Table 2), (2) large catches at low trophic levels (seaweeds, bivalves and other invertebrates), and (3) overfishing,

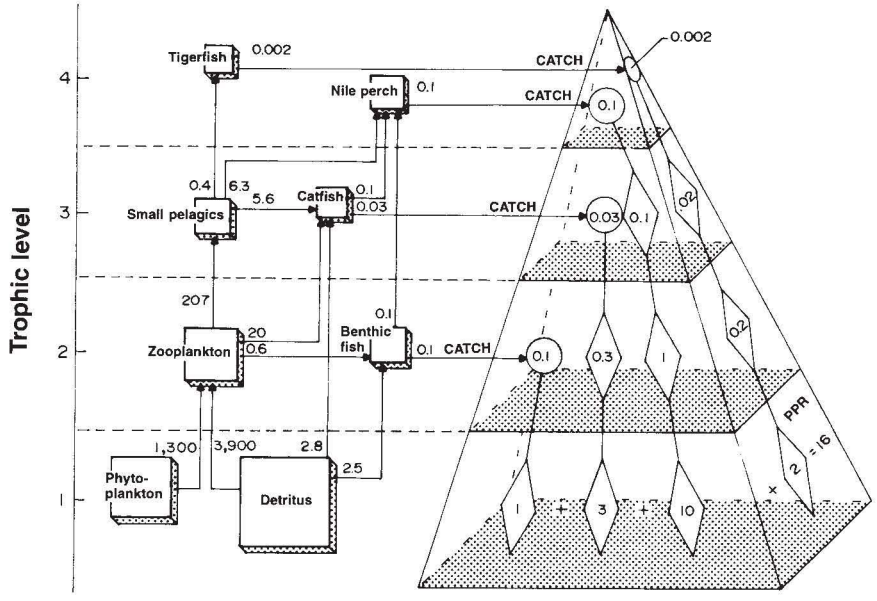

FIG. 1 Schematic representation of approach used here to estimate the PPR to sustain the catches of a given ecosystem. Left, the simplest among the 48 trophic models used here, representing the lightly fished Lake Turkana[18]; each of its state variables (boxes) has inputs (food) and outputs (predation and/or fishery catches), in t wet wt km^{-2} yr^{-1}; only major flows are shown, excluding respiration and back flows to the detritus. Right, the pyramid illustrates how the catches (circles) are raised to PPR at trophic level 1 (diamonds), using the 10% trophic efficiency of Fig. 2.

TABLE 1 Reported world fisheries catches, ancillary statistics and the PPR to sustain these catches

FAO-codes	Species group	Catch (ww; $t \times 10^3$)	n	k	Trophic level Mean	Trophic level s.e.	PPR ($g\,C \times 10^{12}$)
Oceanic (gyre) systems							
36	Tunas, bonitos, billfishes	2,975	1	3	4.2	0.04	523.9
46	Krill	344	—	—	2.2*	—	0.6
Upwelling systems							
35	Anchovies, sardines	11,597	24	97	2.6	0.28	53.1
34	Jacks	4,785	8	28	3.2	0.06	86.7
37	Mackerels	1,096	10	44	3.3	0.10	22.8
57	Squids†	248	6	31	3.2	0.14	6.9
Tropical shelves							
24, 35	Small pelagics	7,127	5	20	2.8	0.27	59.9
31, 33, 39	Misc. teleosteans	5,342	22	16	3.5	0.26	204.3
34, 37	Jacks, mackerels	2,053	8	46	3.3	0.28	45.5
36	Tunas, bonitos, billfishes	1,275	8	44	4.0	0.12	141.7
57	Squids, cuttlefishes, octopuses	1,114	6	31	3.2	0.14	19.6
45	Shrimps, prawns	650	4	21	2.7	0.35	35.0
42–44, 47, 77	Lobster, crabs and other invertebrates	544	7	35	2.6	0.30	2.2
38	Sharks, rays, chimaeras	344	9	51	3.6	0.24	15.2
Non-tropical shelves							
32	Cods, hakes, haddocks	12,209	5	49	3.8	0.25	929.9
33	Redfishes, basses, congers	3,837	2	5	3.4	0.06	110.9
39	Miscellaneous marine fishes	3,362	1	5	3.2	0.11	52.8
34	Jacks, mullets, sauries	2,871	1	3	3.8	0.13	206.0
35	Herrings, sardines, anchovies	2,319	3	8	3.0	0.15	23.7
42–45, 47, 75, 77	Shrimps and other crustaceans	1,195	3	10	2.3	0.24	2.6
57	Squids, cuttlefishes, octopuses†	1,114	6	31	3.2	0.14	19.3
31	Flounders, halibuts, soles	1,098	3	10	2.9	0.12	9.8
37	Mackerels, cutlassfishes	1,096	3	16	3.4	0.29	30.6
23–25	Diadromous fishes	819	14	49	2.4	0.25	2.3
38	Sharks, rays, chimaeras	344	2	15	3.7	0.28	19.2
Coastal and coral systems							
52–56, 58	Bivalves and other molluscs	5,150	4	12	2.1	0.13	7.6
31, 39	Miscellaneous marine fishes	3,424	15	86	2.8	0.41	24.0
35	Herrings, sardines, anchovies	2,319	9	52	3.2	0.20	40.8
9	Seaweeds	1,683	1	—	1.0	—	0.2
34, 37	Jacks and mackerels	1,322	17	97	3.3	0.22	29.3
23–25	Diadromous fishes†	819	3	13	2.8	0.19	5.7
43–45, 47	Shrimps, prawns	748	8	42	2.6	0.33	3.3
42, 74–77	Crustaceans and other invertebrates	566	14	49	2.4	0.25	1.6
72	Turtles	2	2	7	2.4	0.37	0.006
Freshwater systems							
13	Misc. freshwater fishes	5,237	41	273	3.1	0.28	69.4
21–25	Misc. diadromous fishes	1,210	23	121	3.6	0.27	60.1
41, 45, 51, 54, 71, 77	Invertebrates and amphibians	896	14	54	2.2	0.23	1.6
11	Carp-like fish	632	15	79	2.7	0.34	3.7
12	Tilapias and other cichlids	579	24	11	2.5	0.18	2.0

The items used to infer primary production required (PPR) from the reported annual catches (wet weight; means for 1988–1991) were: (1) codes to link the groups in the FAO catch statistics[3] to those in 48 trophic models of ecosystems whose sources are given in Fig. 2; (2) major group names; (3) group catch (total average catches less aquaculture production for 1988 of freshwater, brackishwater and marine fish fed on artificial fish farms, except for India whose annual production of carp-like fishes was assumed at 2×10^5 t), assigned to ecosystem type based on ecological and geographic considerations; (4) mean trophic level (TL), estimated for the groups included in the models in Fig. 2, with standard errors (s.e., in brackets) estimated from $\sum_{i=1}^{k} s_i^2(n_i-1)/(n-k)$ where n_i is the number of prey items used for one estimate of TL, n the sum of all n_i, k the number of TL estimates used to compute each group's mean TL, and the s_i^2 are the variances of these TL estimates, that is, the indices of omnivory[11]; (5) values of n_i and k. The PPR estimates are based on a conservative 9:1 ratio for the conversion of wet weight to carbon[12] and a 10% transfer efficiency per trophic level (Fig. 2), that is, using $PPR = (\text{catches}/9) \times 10^{(TL-1)}$.

* Assumed diet composition 80% phytoplankton, 20% herbivorous zooplankton[10].

† No system specific estimate of trophic level available; instead a value from another system type is used.

which has left the reduced fish biomass unable to use the available production.

The shelf systems exhibit high PPR, from 24.2 to 35.3%, mainly due to industrialized fisheries operating at high trophic levels, a feature in which they differ from upwelling systems, for which, however, the PPR is still high, 25.1% (Table 2). It would seem difficult to further increase these values, especially on temperate shelves, given that a substantial part of the primary production generated during intensive blooms settles out as detritus, before use by zooplankton is possible. Also, higher PPR would starve top predators, such as marine mammals and birds.

Could catches be increased through fishing down the food web, that is, concentrating on fishes at lower trophic levels? In ocean systems, the fisheries targeting tuna would have to harvest the prey of tuna (mainly small pelagic fish), which cannot be done economically at present. In coastal and coral reef systems, fishing has already moved down the food web, and improvements must come from rebuilding biomasses through better management[6,7]. This is also true for tropical shelves, where intensive overfishing is causing significant loss of spawning biomass and of biodiversity, especially through shrimp trawling on soft-bottoms, which results in destruction of soft corals and massive changes in community structure, including large fish being replaced by short-lived organisms (small pelagic fish, cephalopods, jellyfish and so on)[7]. This is aggravated by the fact that, contrary to some terrestrial ecosystems such as rainforests,

TABLE 2 Global estimates of primary production (PP), of PPR to sustain world fisheries (mean for 1988–1991, wet weight), and of the mean trophic levels (TL) of the catches, by ecosystem type

Ecosystem type	Area (10^6 km^2)	PP (gC m^{-2} yr^{-1})	Catch (g m^{-2} yr^{-1})	Discards (g m^{-2} yr^{-1})	TL of catch	PPR (catches + discards) Mean (%)	95% Confidence interval
Open ocean	332.0	103	0.01	0.002	4.0	1.8	1.3–2.7
Upwellings	0.8	973	22.2	3.36	2.8	25.1	17.8–47.9
Tropical shelves	8.6	310	2.2	0.671	3.3	24.2	16.1–48.8
Non-tropical shelves	18.4	310	1.6	0.706	3.5	35.3	19.2–85.5
Coastal/reef systems	2.0	890	8.0	2.51	2.5	8.3	5.4–19.8
Rivers and lakes	2.0	290	4.3	n.a.	3.0	23.6	11.3–62.9
Weighted means (or total)	(363.8)	126	0.26	0.07	2.8	8.0	6.3–14.4

Distribution of surface areas by ecosystem type was estimated based on planimetry, checked against published estimates[13]. As defined here, coastal systems generally reach down to a depth of 10 m, except coral reefs which may reach to about 30 m[14]. The PP estimates are based on ref. 15, with a 1:3 allocation between ocean and shelf productivity[12], and using newer, higher values for upwelling systems[16], leading to a more conservative estimate of PPR. The nutrients released by discarded fish are assumed to have negligible effects on primary production, and on food webs in general[17]. The catches are from Table 1 and their TL are weighted means. The PPR estimates are from Table 1; they were adjusted to account for the discards (allotted across systems based on group-specific catch/discard ratios[4]). Their standard errors (s.e.) were estimated by the Monte Carlo method assuming normal distributions, with the s.e. of the mean transfer efficiencies in Fig. 2, and of the mean TL in Table 1 providing all the variability (10,000 runs per group in Table 1, all within ±1 s.e. of each mean), the FAO catches[3], the discards[4], and the PP by ecosystem type being used as fixed values, notwithstanding their imprecision (see text).

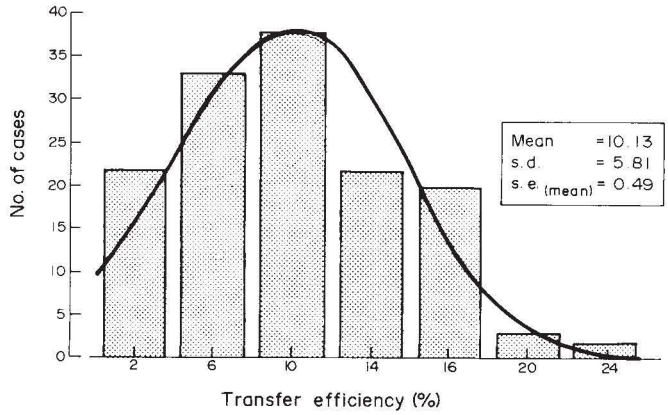

FIG. 2 Frequency distribution of energy transfer efficiencies (TE, in %) in 48 trophic models of aquatic ecosystems. The estimates of TE (N = 140) express, for TL 2 (=herbivores and detritivores) to 4 (=third-order consumers), the fraction of production passing from one TL to the next, and account for consumers feeding on the different TL of an ecosystem[11,19] (no trend of TE with TL was apparent[20]). All 48 trophic models used as sources of TE are fully documented[11,16,21–23]; they jointly show that the 10% TE value commonly used for aquatic organisms[24] is extremely close to the mean of the 140 estimates available for this study.

of which large undisturbed tracts still exist, and contrary to what is stated in the introductory quote, the overwhelming bulk of the world's trawlable shelves is impacted by fishing, leaving few sanctuaries where biomasses and biodiversity remain high.

There is at present a debate about the level of global primary production, which may be slightly higher than the figure we have used[8,9]. However, our fisheries catches are likely to be underestimated as well, despite having been adjusted for discarding practices, because of under-reporting and under-collection, assumed by numerous fisheries scientists, but still awaiting the kind of global analysis now done for discards[4].

Our results, having been obtained by summing independent group- and system-specific catches and PPR estimates, should be robust. Moreover, the estimate of PPR of 8% for all aquatic systems, although nearly four times as high as the previous estimate, masks the important fact that the nearshore systems readily accessible to humans (most upwellings and the shelves), and the freshwater systems have very high PPR, nearing that estimated for terrestrial systems. Because we do not have the ability safely to increase aquatic primary production, these high PPR values confirm broad limits on the carrying capacity of natural aquatic ecosystems, which still form the basis for 85% of the world fish harvest. □

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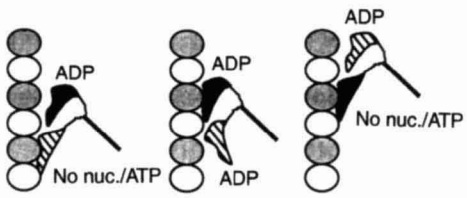

FIG. 4 A model, based on the observed change in angle, of how a pair of kinesin heads could move 8 nm along a tubulin protofilament. Although the spikes that project from the heads in our reconstructed images appear short, the extra protein sequence required to form dimers[25] presumably increases the leverage of the spikes. The simplest way that heads might act alternately over a long distance is for flexible connections to allow them to rotate freely around each other; the direction of movement is determined if, after the attached head changes conformation during ADP release, only the next binding site along the protofilament in the plus direction is within reach of the second head. This model is similar to model A proposed by Hackney[15], except that the angle change accompanies ADP release instead of ATP binding. The kinesin-like protein ncd moves towards microtubule minus ends. If ncd has a similar projecting spike which is tilted in the opposite direction in the strongly bound no-nucleotide and AMP–PNP states, then motility in the opposite direction could be explained by a similar model.

plus end, and thus produce the 8-nm step (Fig. 4). Therefore our results are consistent with a mechanism in which structural changes in the heads result in directional movement. □

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CORRECTIONS

Structure of a new nucleic-acid-binding motif in eukaryotic transcriptional elongation factor TFIIS

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WE previously reported binding of TFIIS residues 231–280 to single-stranded DNA by gel mobility-shift assay (Fig. 1 of this Letter). We have since discovered that the extended form (residues 175–280), rather than the shorter form (residues 231–280), of the protein was inadvertently used in this assay by one of our laboratories (K.A.). The binding of the shorter polypeptide to single-stranded DNA is not reproducible: we therefore retract Fig. 1. Although there is no published spectrofluorometric evidence of interaction between isolated zinc ribbon and nucleic acid, when site-directed mutations in the zinc ribbon domain of the intact protein are used in a stalled transcription assay this domain appears to interact with nucleic acids, as indicated by decrease or elimination of antitermination and RNA cleavage activities[1]. □

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Primary production required to sustain global fisheries

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THERE were several numerical errors published in this Letter, some kindly brought to our attention by M. Baumann and T. R. Parsons (personal communication).

- In Fig. 1, the catch of Nile perch should be 0.01 t km^{-2} yr^{-1} (not 0.1 t km^{-2} yr^{-1}).
- In Table 1, the primary production required (PPR) for squid in the upwelling system should be 4.1, that for shrimps on tropical shelves should be 3.5, and the k value of miscellaneous teleosteans should be 155.
- In Fig. 2, the abscissa should change in steps of 4%.

None of these errors affects the results of our study. □