

Flow Characteristics of Aquatic Ecosystems*

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Abstract

This contribution examines various flow measures based on analysis of 41 quantified models of trophic interactions in aquatic ecosystems. System productivity/biomass ratio is shown to relate to ecosystem maturity and to the degree of cycling in the systems. Distinct patterns or clusters are observed for different types of resource systems with respect to average path lengths and residence times. Examination of the average trophic transfer efficiencies shows efficiencies of 10-11% for herbivores/detritivores and first-order predators, and lower efficiencies for higher trophic levels. The overall average transfer efficiency is 9.2%, and thus confirms the often assumed value of approximately 10% for transfers from one trophic level to the next. An approach for estimation of the amount of primary productivity that is required to produce the biomass which directly or indirectly contributes to the fisheries catches is presented and applied to some of the systems.

Introduction

This paper presents some generalizations based on a selection of the models in this volume along with a number of published ECOPATH models as adopted for comparisons by Christensen (in press). A number of different measures are examined, notably measures discussed by previous authors, and as such, this paper somewhat resembles a collage. Our main intention, however, is to provide some material for comparisons for ecosystem modellers wishing to interpret model characteristics, and for this the present approach seems appropriate. We do not seek to give comprehensive descriptions of all attributes, as the present paper is intended to supplement the contributions of Christensen and Pauly (1992a, b), and Christensen (1992, in press), not to duplicate them.

Methods and Materials

A total of 41 models were used for comparisons in this paper (Table 1). The majority of these are presented in this volume, while a few have been adapted from previously published ECOPATH models (see Appendix 4). The selection of models, along with a few modifications, follow Christensen (in press). Brief descriptions of all models can be found in the same paper. A table giving a summary of the key data can be found in Christensen (1992) though some of the models were updated between that publication and the present.

Very few changes had to be made to the models to facilitate comparison. The models were standardized to using $g \cdot m^{-2}$ wet weight on an annual basis as standard unit, which nearly all also did beforehand. In addition, bacterial activity

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Table 1. Models used for analysis of flow patterns within ecosystems. The model number and filename are used for reference in subsequent tabulations (see also Appendix 4). Where no publication year is indicated under "Source" the reference is to publications included in this volume.

Type and system	Filename	Source
Ponds, lakes and rivers		
1. Mulberry Carp Pond, China	china	Ruddle and Christensen
2. Laguna de Bay, Philippines, 1968	bay68	De los Reyes
3. Laguna de Bay, Philippines, 1980	bay80	De los Reyes
4. Lake Kinneret, Israel	kinneret	Walline et al.
5. Lake Chad, Africa	chad	Palomares et al.
6. Lake Turkana, Kenya, 1973	turk73	Kolding
7. Lake Turkana, Kenya, 1987	turk87	Kolding
8. Lake Victoria, Africa, 1971-1972	victor71	Moreau et al.
9. Lake Victoria, Africa, 1985-1986	victor85	Moreau et al.
10. Lake Tanganyika, Africa, 1974-1976	tanga75	Moreau et al.
11. Lake Tanganyika, Africa, 1980-1983	tanga81	Moreau et al.
12. Lake Malawi, Africa	lmalawi	Degnbol
13. Lake Kariba, Africa	kariba	Machena et al.
14. Lake Ontario, North America	ontario	Halfon and Schito ^a
15. Lake Aydat, France,	aydat	Reyes-Marchant et al.
16. River Garonne, France	garonne	Palomares et al.
17. River Thames, England	thames	Mathews
Coastal areas		
18. Etang de Thau, France	thau	Palomares et al.
19. Tamiahua Lagoon, Gulf of Mexico	tamiahua	Abarca-Arenas and Valero-Pacheco
20. Coast, Western Gulf of Mexico	wgmexico	Arreguín-Sánchez et al.
21. Campeche Bank, Gulf of Mexico	campeche	Vega-Cendejas et al.
22. Shallow areas, South China Sea	thai10	Pauly and Christensen (1993)
23. Lingayen Gulf, Philippines	lingayen	Pauly and Christensen (1993)
24. Schlei Fjord, Germany	schlei	Christensen and Pauly (1992b)
25. Mandinga Lagoon, Mexico	mandinga	de la Cruz-Aguero
Coral reefs		
26. Bolinao reef flat, Philippines	bolinao	Aliño et al.
27. French Frigate Shoals, Hawaii	ffs	Polovina (1984)
28. Virgin Islands, Caribbean	virgin	Opitz
Shelves and seas		
29. Yucatan shelf, Gulf of Mexico	yucatan	Arreguín-Sánchez et al.
30. Gulf of Mexico continental shelf	gomexico	Browder
31. Northeastern Venezuela shelf	venezuel	Mendoza
32. Brunei Darussalam, South China Sea	brunei	Silvestre et al.
33. Kuala Terengganu, Malaysia	terengga	Christensen (1991)
34. Gulf of Thailand, 10-50 m	thai50	Pauly and Christensen (1993)
35. Shelf of Vietnam/China	vietnam	Pauly and Christensen (1993)
36. Deep shelf, South China Sea	deepscs	Pauly and Christensen (1993)
37. Peruvian upwelling system, 1950s	peru50	Jarre et al. (1991)
38. Peruvian upwelling system, 1960s	peru60	Jarre et al. (1991)
39. Peruvian upwelling system, 1970s	peru70	Jarre et al. (1991)
40. Monterey Bay, California	monterey	Olivieri et al.
41. Oceanic waters, South China Sea	oceanscs	Pauly and Christensen (1993)

^aAs modified by Christensen (in press).

was excluded from all models, as they dominated the flows of the five systems in which they were originally included.

The number of groups in the different models and their distribution by trophic level have not been standardized in the present comparisons as this was not necessary for the kind of analyses here (Christensen, in press).

Results and Discussion

System Primary Production/Respiration

Odum (1971) described how the ratio between total primary production and total system respiration (P_p/R) would develop as systems become more mature. For immature systems, he

assumed that primary production would grossly exceed total respiration (e.g., for upwelling systems); he also suggested that the ratio would move toward unity as systems mature. For systems where remineralization is a dominant pathway, respiration was expected to exceed primary production, e.g., for systems receiving large amount of organic pollution. H.T. Odum summarized his description in graphical form, represented here as Fig. 1.

Based on the models given in Table 1, the primary production/respiration ratio can be quantified. However, we found that the estimates were not as nicely distributed around the 1:1 P_p/R line, as one might perhaps have expected (Fig. 2). For the majority of the models primary productivity exceeds respiration. This, however is not surprising as primary production is known to exceed respiration in both oceanic systems (Quiñones and Platt 1991) and coral reefs (Lewis 1981). Table 2 presents a comparison of the literature estimates reported by Lewis (1981) with the estimates from the present study; as might be seen, the two data sets display the same trend, with the bulk of the models having P_p/R ratios in the range from 0.8 to 3.2. However, some of the ECOPATH models show higher values and this warrants a closer examination.

The seven models with the highest P_p/R ratio (numbers 14, 26, 15, 2, 16, 40, 39) are the only ones for which the ratio between total export and the system throughput exceeds 0.3. This points to respiration as the culprit, i.e., to a parameter which, in ECOPATH models is estimated as the

difference between consumption and the sum of production and egestion. Quantification of egestion (or of its converse, assimilation) is often quite uncertain; higher egestion leads to lower respiration and results in a higher production of detritus. As export from the detritus box in ECOPATH models is approximated as the difference between the flow into the detritus box and the flow out of the detritus box, an increased egestion will lead to increased export of detritus. Export of detritus is the only important export for practically all models. Therefore it is evident that the diverging P_p/R ratios are due to problems in model parametrization, specifically problems with quantification of assimilation rates and hence indirectly of respiration.

Adding to the problem of generally high P_p/R ratios is the omission of bacterial activity. Not all the detritus here assumed to be exported will indeed leave the system. Rather, a large fraction of the detritus will be reutilized by bacteria (which respire!) and thus again made available to the systems. Therefore omission of bacterial activity will lead to an underestimation of respiration (and of total throughput). One can thus conclude that ECOPATH-type models from which bacterial activity is excluded, can be expected to overestimate the P_p/R ratios.

System Productivity and Biomass

The ratio of system productivity over biomass (P/B) varies; developing systems tend to have a high P/B ratio, due to low biomasses and high productions, while developed systems tend to

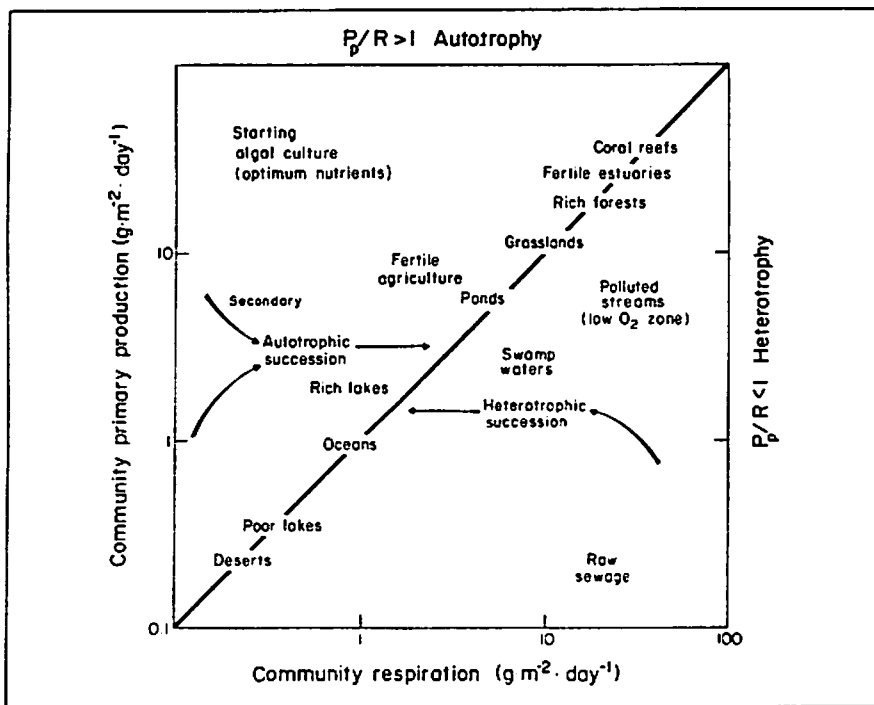


Fig. 1. Position of various community types in a classification based on community metabolism. Gross primary production (P) exceeds community respiration (R) on the left side of the diagonal line ($P/R > 1 =$ autotrophy), while the reverse situation holds on the right ($P/R < 1 =$ heterotrophy). The latter communities import organic matter or live on storage or accumulation. The direction of autotrophic and heterotrophic succession is shown by the arrows. Over a year's average, communities along the diagonal line tend to consume about what they make, and can be considered to be metabolic climaxes. (Redrawn from Odum 1971).

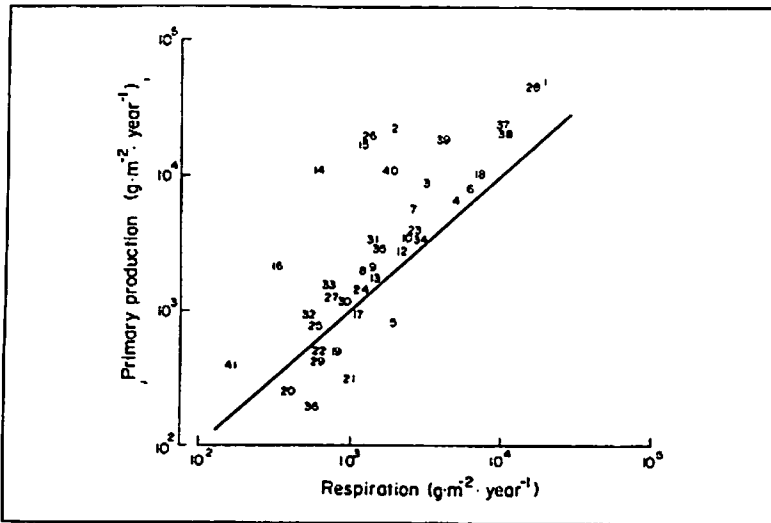


Fig. 2. Total primary production vs total respiration for the 41 models in Table 1, to which the numbers refer. The 1:1 line is indicated.

Table 2. Ratio between total primary production and population respiration as reported by Lewis (1981) and in the present study.

P _p /R Range	Number of systems within the range	
	In Lewis (1981)	In this study
<0.8	1	5
0.8-1.6	9	16
1.6-3.2	12	13
3.2-6.4	3	2
>6.4	0	5

have high biomasses and lower production rates, giving a lower P/B ratios. This relationship was discussed by Margalef (1968) who, working with marine phytoplankton, found that perturbations or fluctuations in the environment cause a shift toward a state resembling earlier phases of ecosystem development.

These findings are however in contrast to those of Baird et al. (1991) who could not identify any relationship between P/B and ascendancy (with ascendancy assumed to be a measure of maturity). Christensen (in press) found that the system P/B ratio was useful as one out of eight attributes for derivation of a maturity ranking. Following Christensen's (in press a) approach, a measure of ecosystem maturity was derived. To obtain some independence, the maturity ranking in the present analysis was, however, derived excluding the system P/B ratio as an attribute. The result is shown in Fig. 3; there is a strong correlation between the two measures; using Spearman's rank correlation gives a highly significant coefficient $r_s = -0.73$.

The maturity ranking was shown by Christensen (in press) to be strongly correlated with total system overheads, which are themselves complementary to relative ascendancy. This means that there are no contradictions in the findings of the three studies discussed.

Pimm (1982) examined the relationship between total primary production and system biomass and found a positive correlation. The analysis of the 41 ecosystem models compared here shows a pattern similar to that found by Pimm (Fig. 4).

Connectance and System Omnivory Index

Connectance is a measure of the observed number of food links in a system relative to the number of possible links (Gardner and Ashby 1970). It has been assumed that there exists an optimum degree of connectance and that this optimum is dependent on the size of the system (Pimm 1982). Other findings suggested that the stability of linear systems decreases as the connectance increases (Martens 1987). Overall the interpretation of connectance is ambiguous.

The system omnivory index expresses the variance in the trophic levels of the consumers prey groups (Pauly et al., this vol.) and can be seen as an alternative to the connectance index. The two indices are here found not to be significantly correlated, and none of them are correlated with ecosystem maturity, as shown by the Spearman rank correlation coefficients, which are not significant.

Pimm (1982) showed that, as the number of groups in a system increases, connectance will decrease. For the present data set, regression analysis gives

$$C = \exp(-0.62 - 0.04 * N),$$

where C is the connectance and N the number of groups in the system. The regression is significant (0.1%), $r^2 = 0.25$. This supports Pimm's findings, but also illustrates that only a small proportion (1/4) of the variability of the connectance can be explained by the number of groups in the system.

Cycling

Cycling is assumed to increase as systems mature (Odum 1969), and can be quantified using Finn's cycling index (FCI, Finn 1976),

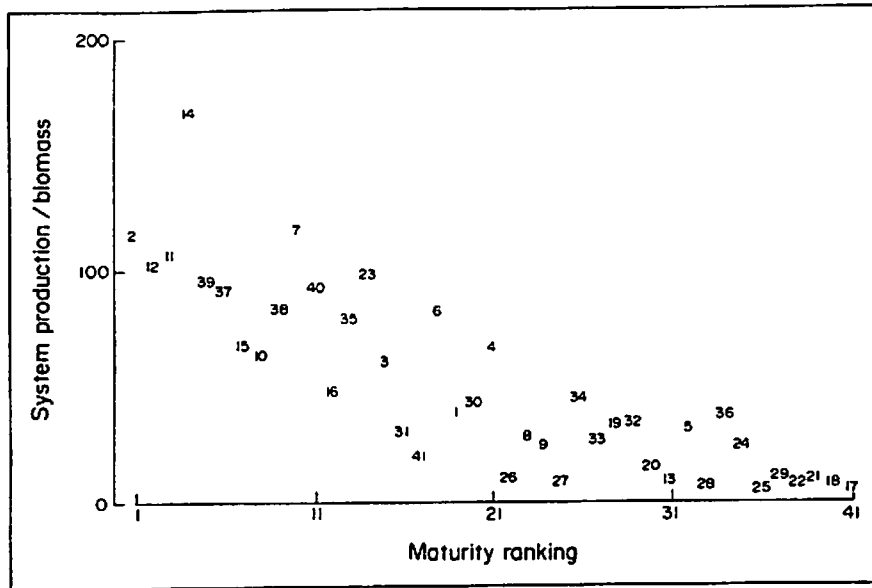


Fig. 3. Relationship between system production/biomass ratio and ranking after maturity *sensu* Odum. The ranking used here was derived without using production/biomass as input.

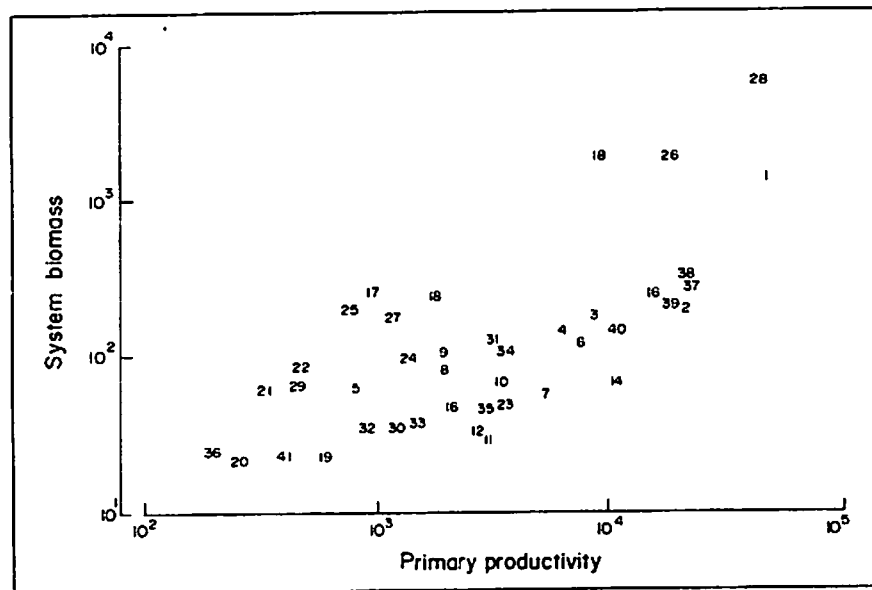


Fig. 4. System biomass as a function of the total primary production for 41 ecosystem models.

which expresses the percentage of the total throughput that is actually recycled. The FCI was not used by Christensen (in press) for quantification of maturity due to its perceived strong dependence on model specification, which makes intersystem comparisons difficult.

However, ranking the systems after both maturity and FCI leads to strong rank correlation ($r_s = 0.56$, $P < 0.1\%$). We conclude from the present analysis that FCI expresses something that is related to maturity.

Richey et al. (1978) compared four North American lakes with different degree of

eutrophication in an effort to evaluate differences in cycling indices, which were found to vary between 0.03 and 0.66. While some of the factors regulating the system structure were apparent, no clear explanations for the varying degree of cycling could be found, suggesting that cycling in itself is not a clear descriptor of ecosystem development.

Wulff and Ulanowicz (1989) and Baird et al. (1991) were more conclusive: in comparisons of ecosystems these authors concluded that FCI was more likely to be an index of stress than of maturity. In both studies, however, it was

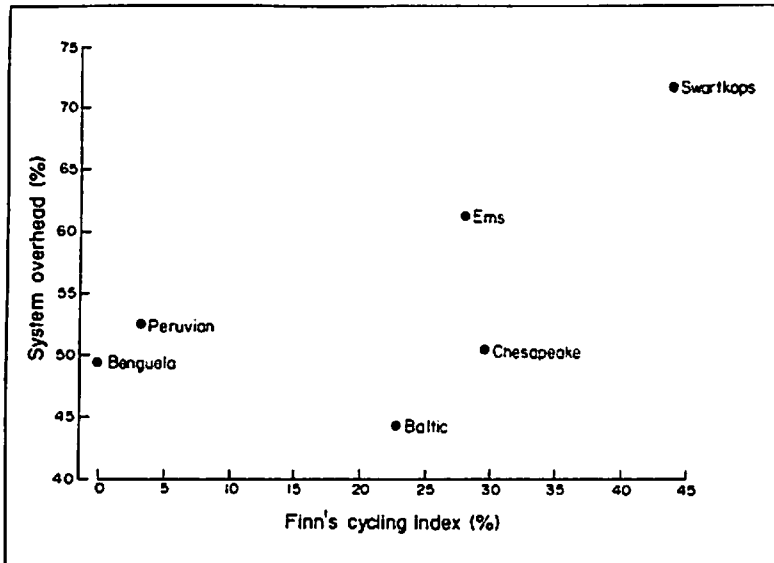


Fig. 5. System overheads (ecosystem stability) vs Finn's cycling index for the six ecosystems studied by Baird et al. (1991).

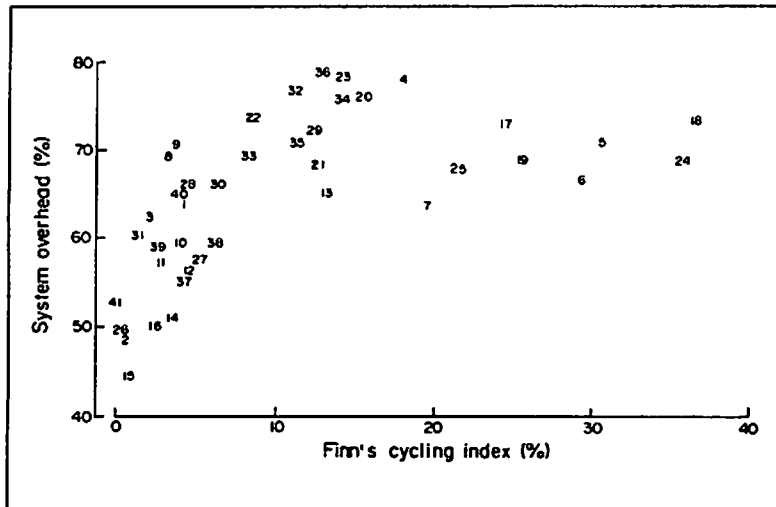


Fig. 6. System overhead (ecosystem stability) vs Finn's cycling index for the 41 ecosystems in Table 3.

assumed that relative ascendancy was itself a measure of maturity, following Ulanowicz (1986).

In contrast, the present analysis suggests that FCI may be related to maturity *sensu* Odum. As maturity was shown by Christensen (1992) to be related to stability *sensu* Rutledge et al. (1976), i.e., to the system overhead (Ulanowicz 1986), one can assume that the FCI also should relate to system overhead.

To study this possibility further, we have first regressed system stability *sensu* Rutledge et al. (1976) against FCI for the six systems studied by Baird et al. (1991).

As can be seen from Fig. 5, this leads to inconclusive results even if the plot indicates that there may be a correlation between FCI and stability. The inconclusiveness is not unexpected,

as only six ecosystems are included, not enough to override the variability of FCI estimates. Cycling is mainly a function of the degree of detritivory and zero-order cycles ("cannibalism") in a system, and both are difficult to quantify.

Studying a larger number of ecosystems can be of interest. Therefore Fig. 6 shows a similar plot for the 41 ecosystems analyzed in this study. There is some correlation between cycling index and system overhead (i.e., ecosystem stability *sensu* Rutledge et al. 1976). The relationship is perhaps parabolic, and suggests that system overheads (stability) decrease at high values of the cycling index. An interpretation may be that ecosystems with low cycling (e.g., upwelling systems) are highly dependent on energy rapidly passing through and as such rather unstable and vulnerable to changes in nutrient input (e.g., through El Niño events). On the other hand, systems with a very high cycling may be less stable because of the need to maintain an intricate pattern of internal flows. Values intermediate of these extremes may well be optimal from a stability point of view.

Cycling and System Overhead

It was demonstrated above that there is a correlation between cycling and system overheads (i.e., ecosystem stability). It is however not clear if this is due to a direct influence of cycling on the system overheads. To study this we

have included a simulation based on the Schlei Fjord ecosystem model (Table 1, No. 24.)

First we removed all cycles from the model, and allocated consumption of detritus to phytoplanktivory. Then we gradually increased the diet component of detritus for zoobenthos from 0 to 60% (the FCI thereby increased from 0 to 22%), by increasing the diet component of detritus for zooplankton from 0 to 60% (the FCI increased from 22 to 26%), and finally increasing the diet component of detritus for both groups from 60 to 99% (the FCI then increased 26 to 31%). This led to the results shown in Fig. 7.

It is clear that there is a relationship between the degree of cycling and these measures. System overhead first increases with cycling, levels off, and finally decreases, to some

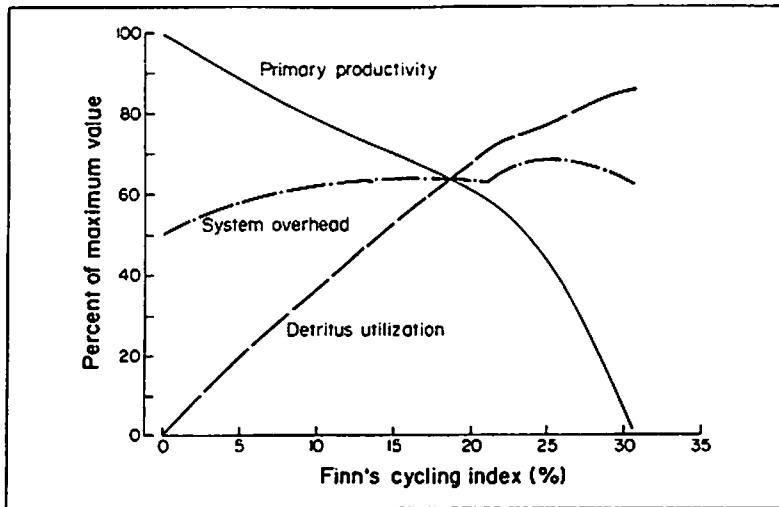


Fig. 7. Relationship among system overhead, primary productivity and detritus utilization, upon the degree of cycling (FCI, all values in %).

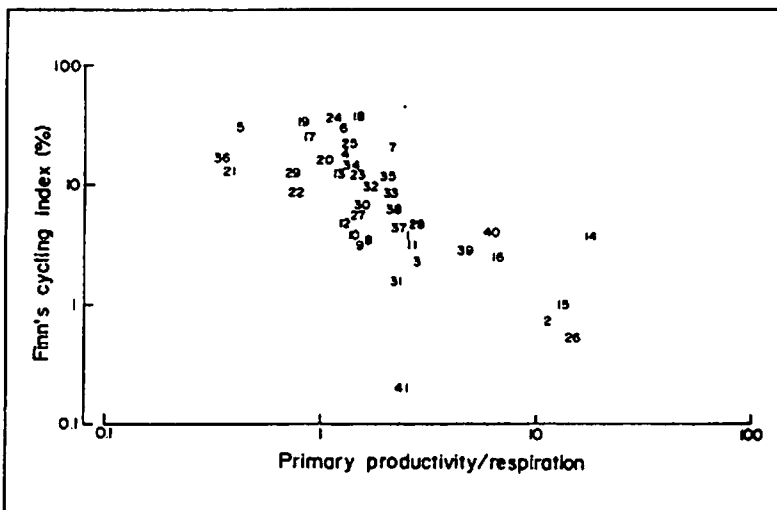


Fig. 8. Finn's cycling index vs primary productivity/respiration ratio for the 41 ecosystem models in Table 1.

extent as on Fig. 6. As primary productivity in trophic models depends on the food consumption of the primary consumers, primary productivity will gradually decline when these consumers shift towards detritivory.

The findings may at first seem alarming because of the lack of robustness that they seem to imply but it should be recognized that unrealistic parametrization is very likely to be detected by careful analysis of the model diagnostics. In the present simulation, primary productivity provides limits for how much cycling can be allowed to vary. It is our conclusion that the results mainly serve to increase our understanding of network indices behavior, and that they do not invalidate the previous findings. This is also supported by the previously reported result of a strong correlation between the path

length and the straight-through path length (Christensen 1992 and see below).

Cycling, Primary Productivity and Respiration

It may be of interest to compare FCI with the primary productivity/respiration (P_p/R) ratio as, based on Eppley (1981), there is an inverse relationship between these indices. A close relationship between FCI and P_p/R does exist (see Fig. 8), and that the only outlier is the model of the oceanic part of the South China Sea (No. 41), a deep (4,000 m) ecosystem dominated by biomasses flow from the surface towards the bottom (sedimentation) with very little recycling.

Fig. 8 shows that groups with a high P_p/R ratio display a low degree of recycling, which is in line with the findings reported above: P_p/R moves toward unity and FCI increases as systems mature. Perhaps the main conclusion to be drawn here is that this indicates robustness and mutual consistency of Odum's (1969) attributes of maturity.

As another system descriptor, we have estimated the average path length for all 41 systems. The path length is defined as the average number of groups that a flow passes through and is calculated as the total throughput divided by the sum of the exports and the respiration (Finn 1980). It appears that average path length is strongly correlated with FCI (Fig. 9). The relationship between cycling rate and path length is not simply a causal relationship from cycling on path length. Christensen (1992) found a strong correlation between path length and straight-through path length for the same 41 models. As the straight-through path length is calculated without reference to cycling this means that the correlation between path length and cycling rate is due to other aspects of the models' structure.

Baird et al. (1991), who compared six ecosystems found that the upwelling systems they studied had short average path lengths; these were longer in the estuarine systems. Fig. 10 was assembled to allow comparisons of the 41 systems studied here.

The majority of the models in Fig. 10 have average path lengths between 2 and 3; 4 have

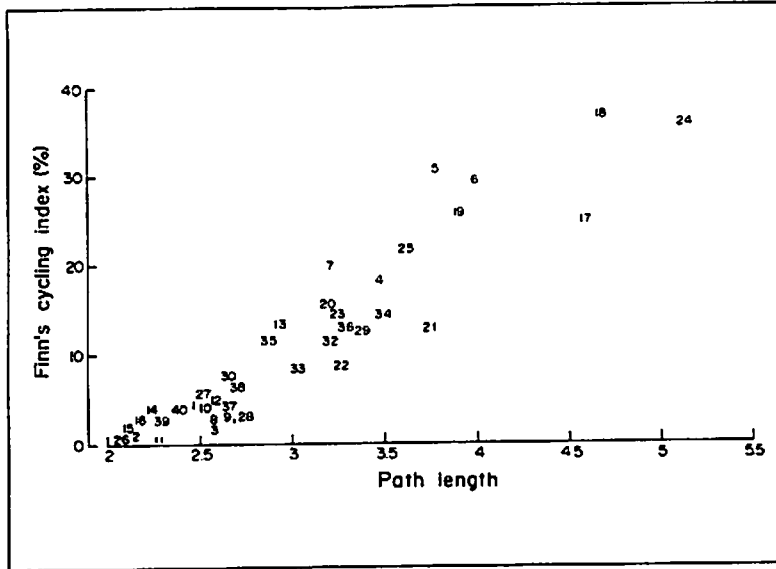


Fig. 9. Finn's cycling index vs average path length for the 41 ecosystem models in Table 1.

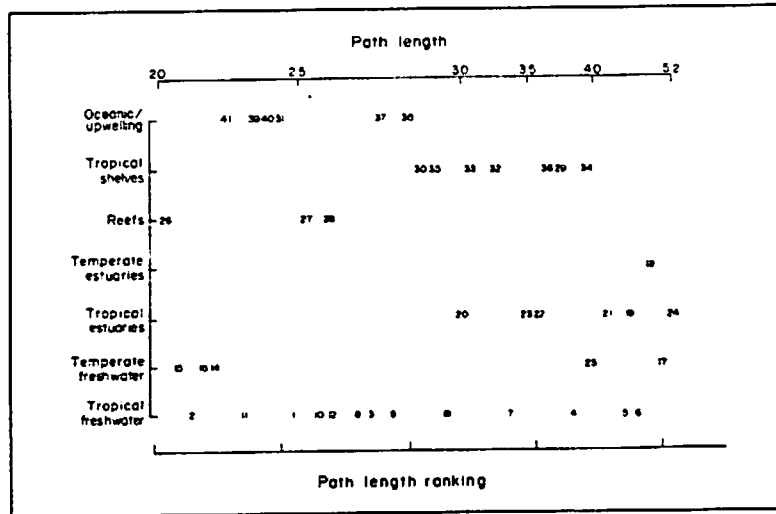


Fig. 10. Tropical and temperate ecosystems ranked after path length.

path lengths between 3 and 4 and only 4 models have path lengths that exceed 4. The estuaries and shelves have long path lengths, and the reefs and upwelling/oceanic systems have short path lengths, which is in agreement with the findings of Baird et al. (1991). The freshwater systems spread out over the scale probably because of "lumping" of ecosystems; the marine systems would do the same had they been pooled in one big "seawater group".

Maximum Chain Length and Trophic Levels

Schoener (1989) discussed the importance of maximum chain length i.e., the number of links in the longest food chain in a system, when one

moves from primary producers or detritus to a top predator. Schoener found from a review of 75 aquatic food webs that only three webs included food chains longer than six steps.

Schoener's results are summarized in Fig. 11 (A-D); this figure also includes maximum chain lengths as calculated from ECOPATH II using the 41 models compared here (E-H). It is evident that the maximum chain lengths in the present study exceed those in Schoener's study.

The differences between the two studies can to some extent be explained by the inclusion of a number of very small systems in Schoener's study, e.g., small rockpools and springs. In contrast the present study includes larger ecosystems. Another reason may be related to how detailed the included diet compositions are in the models that are discussed. Schoener stated, "I see as probably the major problem with web description the decision to draw a link or not. Many species have broad ranges of prey types included in their diet but concentrate on only a few. At what percent occurrence should a prey no longer be counted as such?"

In the models included here, all preys that play a quantitative role (based on weight/volume, not on occurrence) are included. This to some extent reduces the implied degree of subjectivity, but also increases the maximum chain lengths. It is, however, likely that one more explanation must be added to explain the differences: many of the present models are made

by biologists with interest in fish population dynamics, and the upper part of the trophic systems are therefore better described in the present models than in the rockpools and other microsystems in Schoener's study.

The maximum chain length is not always easy to find when the search for food webs is by trial-and-error. Fig. 12 shows the total number of pathways going from phytoplankton to all top predators for the 41 ecosystem models as a function of the number of groups in the systems.

One system shows remarkably many pathways, the Virgin Islands coral reef ecosystem, which includes 107,618 different pathways from the phytoplankton. This astronomical number illustrates that the more one studies diet compositions, the more detailed

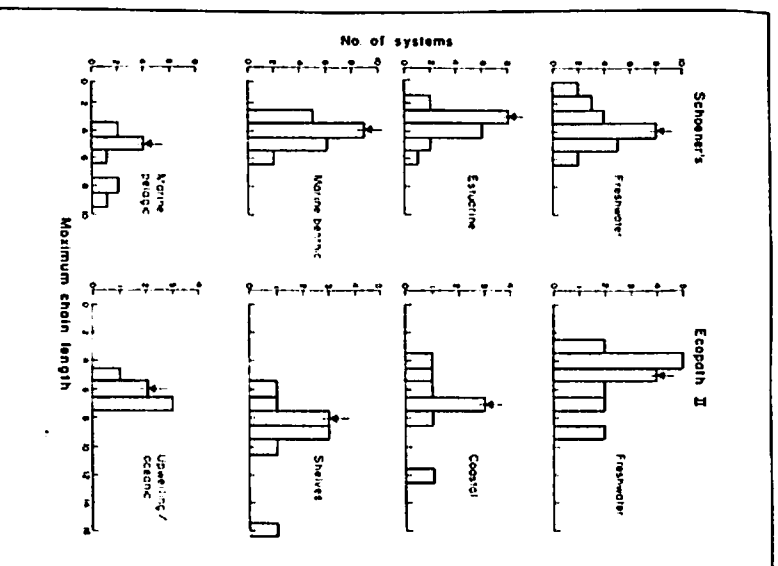


Fig. 11. Distribution of maximum chain length in aquatic systems. The models on the left are adapted from Schoener (1989), while those on the right are based on the 41 models in Table 1. The vertical arrows indicate the median chain length by resource system type.

they will become. For the Virgin Islands system the diet composition was originally based on a very detailed diet matrix with more than 200 different groups, subsequently aggregated to the present 20 box system (Opitz 1991, this vol.).

Given the preceding considerations, it can also be assumed that the more one studies diet compositions, the more trophic levels will appear. Not knowing how much effort the different authors have put into establishing their diet compositions, we have used an indirect approach to examine this relationship: we assume that the degree of effort is reflected in the number of groups in the model descriptions. This led to Fig. 13, where the number of trophic levels has been calculated so that only trophic levels with a throughput of at least $0.1 \text{ gm}^{-2}\text{-year}^{-1}$ are included.

It can be seen that there is a relationship, albeit a weak one, between the two measures. However, none of the systems has more than six trophic levels, which is much in line with Pimm (1982), who could not find systems with more than six trophic levels in the literature. On the other hand the present investigation produced considerably longer food chains than reported by

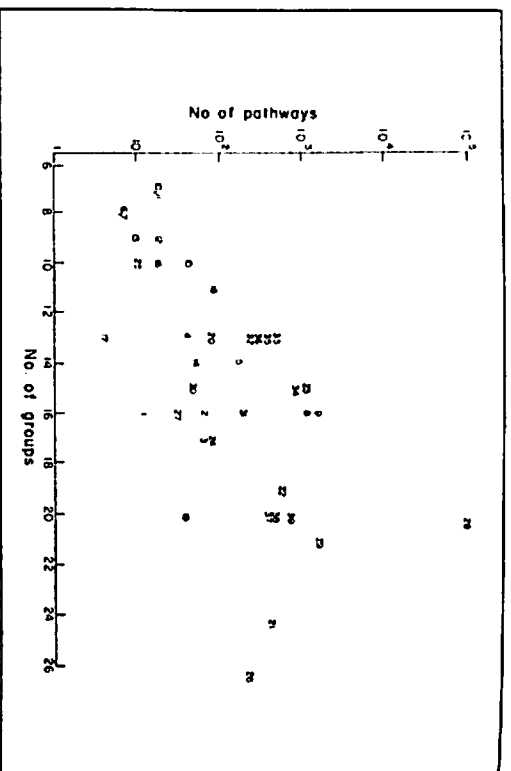


Fig. 12. Number of pathways from phytoplankton to all top predators as a function of number of groups included in description of 41 ecosystem models in Table 1.

either Schoener (1989) or Pimm (1982), and it is likely that this is best explained by the generally larger size of the ecosystems considered here, along with more detailed descriptions of food compositions.

The distribution of number of trophic levels for models belonging to different resource systems is presented in Fig. 14. The average number of trophic levels is lowest in the freshwater systems and increases from coastal systems over reefs to shelf systems, and declines for the upwelling systems. Nothing much is available for comparison with these findings, but Ryther (1969) found that food chains in upwelling areas are shorter than in open oceans systems. This trend is not found in the present study, where the number of trophic levels, and the maximum and average food chain lengths of the upwelling systems exceed those of the oceanic systems. This may well be explained by the more detailed description of trophic interactions in upwelling areas included here, compared to previous descriptions.

Pimm (1982) made several "predictions" for testing purposes. One of these was that "sites with high primary productivities should have more trophic levels than those with low productivities." Pimm reviewed the available cases and refuted the prediction. This is also the result of analysis of the 41 ecosystem models in this study. There are no indications at all of a correlation between productivity and the number of trophic levels in a system.

Residence Time

Overall residence time of particles or energy in the system can be estimated from the ratio of

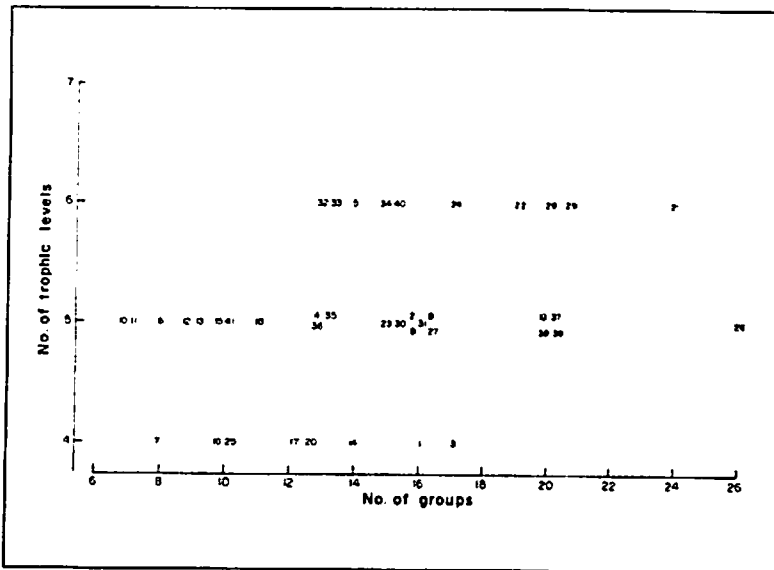


Fig. 13. Number of trophic levels as a function of number of groups in the model descriptions for the ecosystems included in this study.

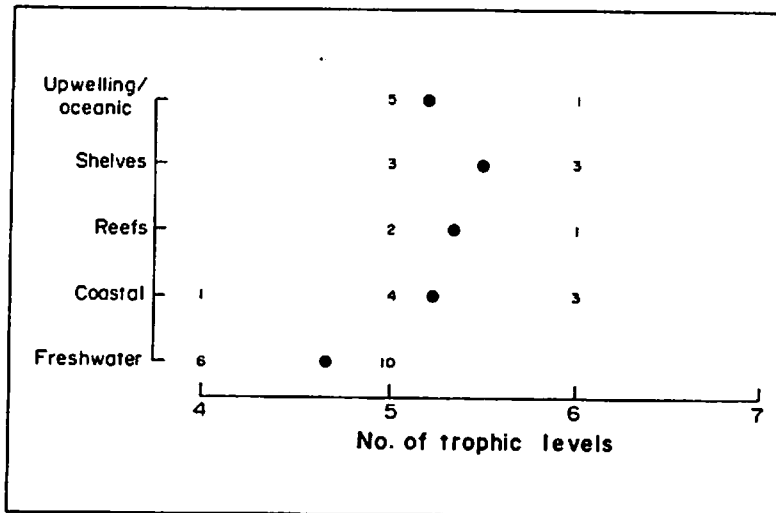


Fig. 14. Number of systems with a given number of trophic levels, by resource system type. The dots indicate means.

total system biomass to the sum of all respiratory flows and all exports (Herendeen 1989). It has been assumed that the residence time of particles on energy in a system increases to a maximum during succession as a result of increasing ecological organization (Cheslak and Lamarra 1981).

Overall residence time has been estimated for the 41 models compared here, and used for quantification of ecosystem maturity (Christensen, in press a). The residence times for the models (Fig. 15) vary from a few days to a quarter of a year.

To help in the search for patterns in residence times Fig. 15 also shows the ecosystems ranked after increasing residence time, and grouped in different resource types. This suggests

that upwelling systems generally have a short residence time, while shelves generally show long residence times. The coral reefs also have long residence times, along with most of the estuarine systems, while the freshwater systems dominate the short residence time end of the ranking.

Trophic Transfer Efficiencies

Since Lindeman (1942), it has often been assumed that trophic transfer efficiencies in ecosystems vary around 10%, so that one-tenth of the energy that enters a trophic level is transferred to the next trophic level; and that the trophic transfer efficiencies gradually decrease on the higher trophic levels due to increased respiration (Lindeman 1942; Burns 1989).

Numerous approaches have been suggested for calculation of trophic transfer efficiencies. Originally, they were calculated as net energy intake less respiration relative to the net energy intake (Lindeman 1942, based on G.E. Hutchinson, unpubl.); alternatively they may be based on ratios such as total transfer to the next higher trophic level over total transfer from the previous lower trophic level.

In the present analysis a definition intermediate between the above two has been adopted: the ratio between the summed exports and predation, and the energy throughput (total consumption) on a given trophic level (Christensen and Pauly 1992b). Following this definition only the proportion of the production that is lost to the detritus is excluded from the calculation, and fishery or harvesting activities are treated as "predators" in the system. Efficiencies for the producers, trophic level 1, are not quantified in the present analysis, as all models are on a wet weight basis, and their (solar) energy input is therefore not quantified.

Using the trophic aggregation routine in ECOPATH II (Christensen and Pauly 1992a) the flows in a system can be distributed by trophic levels and the transfer efficiencies can be estimated. The approach follows one originally described by Ulanowicz (in press).

The trophic transfer efficiencies depend strongly on how the efficiencies of the groups in a system are described. High gross food

Table 3. Trophic transfer efficiencies (%) for a number of ecosystem models. Only trophic levels with a throughput of at least $0.01 \text{ g m}^{-2} \text{ year}^{-1}$ and quantified fisheries catches are included.

		System								
Trophic level	1	2	3	4	5	6	7	8	9	
	Pond China	Laguna 1968	Laguna 1980	Kinneret Israel	Chad Africa	Turkana 1973	Turkana 1987	Victoria 1971-72	Victoria 1985-86	
2	5.3	9.8	5.6	19.6	8.8	8.7	4.4	16.0	15.9	
3	12.4	23.1	19.4	8.4	12.6	1.6	5.4	12.3	18.6	
4	13.9	16.7	18.2	3.8	11.5	2.6	0.8	7.0	10.5	
5	-	16.9	-	3.2	9.8	0.8	-	5.4	10.8	
6	-	-	-	-	8.5	-	-	-	-	
	10	11	12	13	14	15	16	17	18	20
	Tanganyi. 1974-76	Tanganyi. 1980-83	Malaŵi	Kariba	Ontario N.America	Aydat France	Garonne France	Thames England	Thau France	Coast Mexico
	18.3	13.8	16.9	5.4	4.7	6.6	10.1	8.3	5.3	17.5
	8.6	11.5	2.5	6.5	5.6	2.9	5.3	1.4	13.9	18.6
	10.1	11.0	1.6	2.0	4.2	14.1	0.2	0.0	17.3	12.9
	11.2	11.3	0.0	2.2	-	5.6	-	-	16.4	10.0
	-	-	-	-	-	-	-	-	-	8.0
	21	22	23	24	26	27	28	29	30	31
	Campeche Mexico	Coast SCS	Lingayen Phil.	Schlei Germany	Bolinao Phil.	FFS Hawaii	Virgin Island	Yucatan Mexico	G.o. Mexico	Venezuela
	18.4	6.3	9.4	4.9	9.1	10.1	15.7	15.7	7.6	10.5
	16.8	3.6	10.9	10.3	11.9	4.0	9.5	19.7	15.1	9.1
	13.6	14.6	24.0	8.2	10.3	4.1	6.2	17.6	8.1	4.1
	12.2	15.8	26.8	-	10.8	3.3	6.1	15.4	4.9	6.0
	11.7	-	29.6	-	-	-	7.7	8.3	-	-
	32	33	34	35	36	37	38	39	41	
	Brunei D.	Malaysia	G.o. Thailand	Vietnam	Deep SCS	Peru 1950s	Peru 1960s	Peru 1970s	Ocean SCS	
	15.9	22.7	7.2	3.5	10.8	2.6	2.9	9.3	9.2	
	18.7	17.8	15.5	11.7	12.4	9.8	10.6	15.1	12.1	
	12.2	14.0	9.7	10.3	9.0	1.8	1.9	7.0	8.0	
	6.6	16.2	10.8	7.5	9.0	1.0	0.1	2.4	7.2	
	3.5	17.5	13.6	-	-	-	-	-	-	

two unexploited reef systems show highest efficiencies for the herbivores/detritivores, and lower on the higher trophic levels.

For the tropical shelf areas some of the models from Southeast Asia show high transfer efficiency. This is partly due to high exploitation rates, but it may also be caused by similarities in model construction; this is most apparent for the Malaysian model, whose parameter values were used in a number of the other models from the region, including the Lingayen model mentioned earlier to have excessively high efficiencies.

The transfer efficiencies for the upwelling systems and the oceanic system in Table 3 suggest a pattern of low herbivore transfer efficiencies, higher efficiencies on trophic level 3 and lower efficiencies on the higher levels. It is noteworthy that the transfer efficiencies of the Peruvian system increased from the 1950s, over

the 1960s, to the 1970s. This increase may be due to the collapse of the anchoveta (*Engraulis ringens*) and the high exploitation rate (see Jarre-Teichmann 1992 for further discussion).

The two offshore South China Sea models show the same patterns, but as expected the efficiencies are higher in the model covering the more shallow part (Deep SCS). The match between the trends is not likely to be caused primarily by similarities in the model descriptions, but more likely reflects the actual situation.

Based on the system and trophic level specific transfer efficiencies the average transfer efficiencies for the different systems can be estimated (as geometric mean, weighted after flow). As expected the African lakes fall in two groups: high and low efficiency systems, with average efficiencies of 10-15% and of 2-8%

respectively. The distribution of systems on these groups is as discussed above.

The three temperate systems, rivers and fjords have rather low average efficiencies, from 3 to 7%, while the single temperate lagoon has an average efficiency within the range of the tropical lagoons and coastal systems, i.e., between 10 and 14%. Two coastal areas/shelves, Lingayen Gulf, and Kuala Terengganu, Malaysia, both have very (unrealistic) high efficiencies, 17-18%, probably because of similarities in the model descriptions. These systems are not used in the later generalizations.

The coral reef systems have average efficiencies in the range of 5-10%, while the models for the deeper tropical shelf areas generally have average efficiencies of 5 to 10%, only the deeper part of the Gulf of Thailand has a higher efficiency (12%).

The deeper part of the South China Sea and especially the Peruvian upwelling models are also to be found below the 10% efficiency line.

It is difficult to present conclusions regarding overall trends for ecosystems based on the very variable observed efficiencies. One overall system level property can however be estimated: the overall average transfer efficiencies by trophic level based on the 36 models that are discussed here. Fig. 16 shows an average efficiency of 10% for the herbivores/detritivores, 11% for the next trophic level and lower efficiencies (7.5-9.0%) on the higher trophic levels. The grand mean transfer efficiency for all trophic levels in all systems is 9.2%, so Lindeman was not far off.

It can be concluded that the trophic transfer efficiencies are variable, because of both system- and model-specific characteristics. Generally, the trophic efficiencies at lower levels (2, 3) tend to be higher than at higher levels (4-6). In addition, the grand mean trophic transfer efficiency is found to be very close to the often assumed, but rarely estimated, general rule of 10% per step up the trophic ladder.

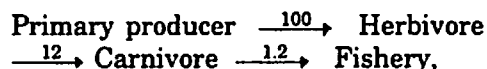
Primary Production Required for the Fisheries

For terrestrial systems, it has been shown by Vitousek et al. (1986) that nearly 40% of the potential terrestrial net primary productivity is used directly or indirectly by human activities. Similar estimates for aquatic systems are not available though a rough estimate was presented in the same publication. The figure given was 2%, i.e., much lower than the estimate for the terrestrial systems. It was based on the

assumptions that the "average fish" feeds two trophic levels above the primary producers; and that the average food conversion efficiency is 10% at each trophic level.

The crudeness of the approach for the aquatic systems is due to lack of information especially on the trophic positions of the various organisms harvested by humans. Models of trophic interactions may, however, help to alleviate the situation, and we suggest here an alternative approach based on network analysis, for quantification of the primary productivity needed to sustain harvest by humans.

This approach is based on quantified descriptions of trophic flows in ecosystem networks. First, all cycles are removed from the diet compositions, and all paths in the flow network are identified using the method suggested by Ulanowicz (in press). For each path the flows are then raised to primary production equivalents using the product of the catch, the consumption/production ratio of each path element times the proportion the next element of the path contributes to the diet of the given path element. For instance for a path,



the primary production equivalents corresponding to the catch of 1.2 units are: $1.2 \cdot [(12/1.2) \cdot 1] \cdot [(100/12) \cdot 1] = 100$, as expected for this simple straight food chain.

This approach (which will be implemented in future releases of ECOPATH II) was applied to some of the ecosystems analyzed in this volume, and the results follow.

For the Peruvian upwelling ecosystem, the harvest in the 1950s required 2% of the available primary productivity (PP). In the 1960s, the fishery expanded drastically (14 times) while the primary productivity requirements (PPR) increased to 5%. The relatively small increase in PPR is mainly caused by the increased catch being predominantly anchoveta which is phytoplanktivorous, and thus require comparatively less PP than organisms on higher trophic levels. The model estimate for the model for the Peruvian system in the 1970s pointing to this model being parametrized with an unrealistically low production/biomass estimate for bonito (0.03 year^{-1}). This indicates that the present analysis may be used as a sensitive tool for model diagnosis.

For the Laguna de Bay models, total PPR increased slightly from the late 1960s to the early 1980s (from 892 to 941 t ww km⁻² year⁻¹). Total PP, however, decreased considerably due to the

milkfish's consumption of phytoplankton resulting in an increase in utilization of PP from 4 to 11%.

In Lake Victoria, the proliferation of Nile perch resulted in a threefold increase in PPR, to sustain the catches, from some 242 t ww km⁻² year⁻¹ in the model from the early 1970s to 742 t ww km⁻² year⁻¹ in the model for the mid-1980s.

For many of the coastal tropical ecosystems the PPR is of the order of a few percentage of the total PP, e.g., for the Brunei, Bolinao and Vietnam models and for the shallow part of the Gulf of Thailand ecosystem. Interestingly, the PPR is higher for the offshore part of the South China Sea (up to as high as 32% for the deep South China Sea models). The catches in the offshore regions are mainly of large pelagics high in the food web, and thus indirectly requiring a large fraction of primary productivity.

The method we are proposing here for study of PPR to sustain catches to some extent parallels a methodology and a concept for valuation of flows in an ecosystem: emergy, short for embodied energy, developed by Odum (1988). Using the emergy concept, it is possible to assign a value to all transfers and for instance compare how export and import of natural resources from a country compare. The basic principle is that using flow specific transfer coefficients all flows are given in a common currency expressing how much energy was used to generate the flows. The currency in the applications we know of has been solar energy equivalents, see e.g., Brown et al. (1988), and Brown and McClanahan (1992).

The present cursory treatment only gives a first rough introduction to what can be achieved from studies of that part of primary productivity that is used by humans. We anticipate that further studies will be of use for strategic considerations related to our global use of ecological resources.

Conclusion

The present analyses have shown that it is possible, based on quantified ecosystem models, to estimate characteristics of flow patterns in aquatic ecosystems. We hope that this preliminary study will encourage new studies aimed at further refining the analyses, and placing these in a context where the information can be utilized in a management context. Most notably the question of how ecosystems are best utilized needs proper attention. For this, estimation of ecosystem flow patterns is of prime concern.

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