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CHANGES IN MODELS OF AQUATIC ECOSYSTEMS APPROACHING CARRYING CAPACITY

VILLY CHRISTENSEN[1] AND DANIEL PAULY[1,2]

[1]*International Center for Living Aquatic Resources Management, M.C. P.O. Box 2631, 0718 Makati City, Philippines*
[2]*Fisheries Centre, University of British Columbia, Vancouver, British Columbia*

Abstract. Using a top-down modeling approach, published mass-balance models of trophic interactions and state variables in the western central Pacific Ocean and the northern Gulf of Mexico shelf were used to explore how large increases in top predator biomasses can be accommodated with given primary productions. It appears that the biomasses of top predators in these models can be increased an order of magnitude, which leads to a six- to sevenfold increase in overall consumer biomasses. This results in changes in food web structures that are in agreement with major aspects of E. P. Odum's theory of ecosystem development, particularly with regard to features associated with the retention and recycling of detritus. Based on the simulations and Odum's theory, we propose a functional definition of carrying capacity: the upper limit of biomass that can be supported by a set primary production and within a variable food web structure is reached when total system respiration equals the sum of primary production and detritus import. The theory supported by the simulations has a number of corollaries relevant to sustainable management of ecosystems.

Key words: carrying capacity for aquatic ecosystems; detritus recycling; ecosystem development; ecosystem models; Odum's theory of ecosystem development; primary productivity, utilization; retention and recycling of detritus; trophic models.

INTRODUCTION

Humans have fished the seas for thousands of years. The implicit rule has been to ''fish down the food web'' by initially targeting the larger, predatory fishes, and, as these become more scarce, gradually shifting to smaller and smaller species and individuals. In parallel, the marine mammal populations that once dominated the oceans have largely been driven toward extinction. We may speculate, then, on how the seas and oceans were before the fishing and whaling started; a good guess is that the biomasses of both predator and prey species were much greater than at present (MacIntyre et al. 1995, Pauly 1995). If we knew how much greater the biomasses might have been back then, or how great they theoretically could be now, we would have—under optimistic assumptions regarding reversibility of certain trends—an estimate of the carrying capacity of the systems in question. Such limits could be used to design new schemes of ecologically sound exploitation patterns that could probably sustain much higher yields and biodiversity than at present.

ECOSYSTEM DEVELOPMENT

E. P. Odum (1969) formulated a cohesive set of hypotheses to predict the long-term response of ecosystems over evolutionary time (or under stress) that incorporates elements of trophic links, of size, of (bottom) structure, and of communities of species. He described how systems tend to develop toward maturity over time, how ecosystems change when stress is applied to them, and discussed how this would be reflected through 24 attributes of ecosystem maturity, a selection of which is presented in Table 1.

Odum (1969) used the maturity concept to describe a wide range of ecosystems, from microcosm cultures to forests. Important here is that their development is not, and need not, be deterministic. Hence, the specific trajectory of an ecosystem following perturbations is not determined. However, the theory states that it will develop so that the trends indicated by the attributes of ecosystems (Table 1) are followed. For the purpose pursued here this is what is called for.

The key tenets of Odum's theory have been much debated since its publication. This is only what must be expected: major theories offer a wide range of ideas to attack and attackers need not assess whether the counterclaims, jointly, make as much sense as do the interrelated parts of the theory under fire. As was pointed out by Odum (1977), ''we like to think that setting up radical but testable hypotheses at the beginning had much to do with this progress. Scientists work together best when motivated by some common idea, even if—or perhaps, especially if—that idea is controversial.''

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TABLE 1. A selection of Odum's 24 attributes of ecosystem maturity. Characteristic values for ecosystems in developmental or mature stages are presented for the selected attributes.

	Ecosystem attributes†	Developmental stages	Mature stages
1	Gross production/respiration	>1 or <1	Approaches 1
2	Gross production/biomass	High	Low
3	Biomass supported/energy flow	Low	High
4	Net community production	High	Low
6	Total organic matter	Small	Large
12	Niche specialization	Broad	Narrow
13	Size of organism	Small	Large
15	Mineral cycles	Open	Closed
16	Nutrient exchange rate between organisms and environment	Rapid	Slow
17	Role of detritus in nutrient cycling	Unimportant	Important
21	Nutrient conservation	Poor	Good
22	Stability (resistance to external perturbations)	Poor	Good

† Only attributes that can be quantified using trophic mass-balance models are included. The numbering refers to Odum's (1969) original numbering.

Proper testing of a theory is often facilitated if the theory can be expressed in quantitative terms. However, neither Odum nor his detractors quantified more than a few of the attributes in Table 1. An approach described by Christensen (1995)—the construction, analysis, and comparisons of mass balance trophic models of ecosystems—can be used to quantify the attributes in Table 1, and, hence, be used for testing purposes.

METHODOLOGY AND HYPOTHESES

The Ecopath model was originally described by Polovina (1984) and was further developed by Christensen and Pauly (1992*b*). It is structured around a system of linear equations for expressing mass-balance, which, in its simplest form, can be expressed for an arbitrary time period and for each element *i* of an ecosystem by:

$$B_i \cdot (P/B)_i \cdot \mathrm{EE}_i = C_i + \sum_{j=1}^{k} B_j \cdot (Q/B)_j \cdot \mathrm{DC}_{ij} \qquad (1)$$

where B_j is the biomass of *i* during the period covered (conventionally, a year); $(P/B)_i$, its production/biomass ratio; EE_i, its ecotrophic efficiency, i.e., the fraction of the production that is utilized within the system for predation or export; C_i, the fisheries catches (if any); B_j, the biomass of each of the *j* predators of *i*; $(Q/B)_j$, the relative food consumption of *i*; and DC_{ij} is the fraction of *i* in the diet of *i*.

Although perhaps not immediately obvious, the system of linear equations in Eq. 1 defines many of Odum's attributes, mainly through the system of fluxes linking the state variables (Christensen and Pauly 1992*a*). Thus, based on comparisons of the attributes in Table 1 amongst 41 ecosystems, Christensen (1995) showed that these attributes, indeed, jointly describe what Odum calls "maturity," a theme to which we shall return.

Here we will use the Ecopath approach to address a question related to Odum's theory: what if the biomasses of top predators in representative marine systems were much greater than presently observed?

Based on anecdotes, historic biomasses of commercial fish species may well have been 10–20 times higher than they are now (MacIntyre et al. 1995). We have no means, however, of describing the nature of the ecosystems before humans interfered. We have enough problems, even with extensive sampling, doing that for today's fished systems. Still, we can address some questions about earlier climax systems through model simulations:

1) Is it possible to accommodate much higher biomasses of top predators and of necessary prey given the present levels of primary production?

2) Are the changes in system structure that would result from Question 1 in accordance with the theory for ecosystem development put forward by E. P. Odum?

3) How does the limit for top predator biomasses relate to the carrying capacity concept?

4) Are there lessons to be learned that are of interest for ecosystem management?

We will address these questions using a top-down simulation based on two published mass-balance models of exploited marine ecosystems. One represents the Eastern Central Pacific (Trites et al., *in press*), where tunas are directly exploited and where the biomasses of marine mammals are known to have been much reduced through whaling, and for dolphins by drowning during purse-seining operations. The second model (Browder 1993) represents the northern shelf of the Gulf of Mexico, where fisheries have much reduced the abundances of various top predators (marine mammals, tuna, sharks, etc.). A brief summary of some of the major characteristics of the two models is given is Table 2.

The starting point for the simulations was a trophic model with mass balance. The biomasses of the top predators were then increased and catches set to zero. The biomasses of the intermediate consumers (all consumers that are not top predators) were estimated so as to ensure sufficient food supplies for the top predators. This was done based on the assumption that 95% of the production of all of the intermediate consumer groups were utilized in the ecosystem (which is the same as assuming EE to be 0.95 in Eq. 1). This reflects the fact that in marine ecosystems most of the production is used for predation or fishery; very few organisms die from old age, diseases, etc. All basic pa-

TABLE 2. Ecological groupings in the Eastern Central Pacific ecosystem model (Trites et al., *in press*), and the model of the northern continental shelf of the Gulf of Mexico (Browder 1993). Each model also incorporates a detritus group to which all excreta and dead organisms are directed.

	Eastern Central Pacific model		Northern shelf of Gulf of Mexico model	
Type	Group	Biomass†	Group	Biomass†
Top predators	Tuna, billfish	0.05	Marine mammals	0.020
	Marine mammals	0.14	Tunas	0.044
			Billfish	0.005
			Sharks	0.082
Intermediate consumers	Misc. fish	0.50	Pelagic predators	0.046
	Benthic fish	1.5	Demersal predators	0.68
	Mesopelagics	2.6	Demersal fish	3.5
	Small pelagics	1.9	Mackerels	0.13
	Large squids	0.46	Pelagic fish	12.5
	Small squids	0.96	Crabs, shrimps	1.0
	Benthic invertebrates	5.0	Benthic invertebrates	5.0
	Large zooplankton	10.0	Zooplankton	3.6
	Small zooplankton	3.3		
Primary producers	Phytoplankton	(882)	Phytoplankton	(1190)
			Benthic producers	(30)

† Biomasses (wet; g/m^2) are given for all consumer groups; the production (wet mass; g·m^{-2}·yr^{-1}) is given for the producers.

rameters (biomass, production/biomass ratio, and consumption/biomass ratio) were allowed to vary within ±20%, while the diet fractions were allowed to vary ±0.1, (e.g., from 0.25 to 0.45 if the original diet estimate was 0.35). For zero-order cycles in the diet (''cannibalism''), and for prey items contributing $\leq$0.01 to a diet, the diet components were allowed to vary ±20%. Primary production of wet mass was fixed at its original levels, i.e., at 880 g·m^{-2}·yr^{-1} and 1220 g·m^{-2}·yr^{-1} in the Pacific and Gulf of Mexico models, respectively.

Using a Monte Carlo technique, incorporated in Ecopath (Christensen and Pauly 1995) parameter, distributions were sampled randomly and 1000 runs with thermodynamically acceptable results were made for both of the original models (which we refer to as ''Now''), and for each of those with increased top predator biomasses. Models were rejected if they did not meet the mass-balance requirements defined in the Monte Carlo routine (all EEs $<$1; all production/consumption ratios $<$0.6). Comparisons of ecosystem attributes were based on the mean values from all accepted runs.

Trophic transfer efficiencies were calculated based on an approach described by Ulanowicz (1995), in which the trophic groups in a network were aggregated in discrete trophic levels (sensu Lindeman [1942]) based on the food web structure. The transfer efficiencies for each trophic level were next calculated as the percentage of throughput entering a trophic level that is subsequently passed on to the next trophic level or harvested. The routine for the computations was incorporated in the Ecopath software.

QUEST FOR A MATURE SYSTEM

The Eastern Central Pacific Ocean

The main result of the simulation is that a 10-fold increase of tuna and marine mammal biomasses can easily be accommodated within the system. This was achieved mainly because the Monte Carlo routine selects a better utilization of the detritus, which, in the present day model, mainly leaks out of the system. In contrast, the detritus is largely recycled in the model with increased top predator biomasses. Applying Finn's (1980) cycling index, we find that 25% of the energy throughput is due to recycling in the top predator-enriched model, as compared to 2% in the present state model (Table 3).

To address Question 2, we may take a look at the behavior of those attributes of ecosystem development that could meaningfully be quantified using mass-balance models (Table 3). As may be seen, the trends observed in all attributes are in accordance with Odum's theory of ecosystem development.

Some interesting changes concern total consumer biomasses (of which the top predators account for only 1%) which increased by a factor of six due to cascading effects to all trophic levels (Table 3). Further, the simulations show that mean trophic transfer efficiency increased from 12% in the original model to 16% in the modified model (Table 3).

The Gulf of Mexico northern continental shelf

To see if the agreement between the model simulations for the Eastern Central Pacific and Odum's theory of ecosystem development was an isolated incidence, we repeated the simulation procedure on a trophic mass-balance model for the northern continental shelf of the Gulf of Mexico described by Browder (1993). Here the original model was slightly modified. Originally, small pelagics were assumed to have a production rate of only one-fourth that of the top predators and a gross food conversion efficiency of only 3%. These values are not very realistic, so the production rate was calculated from a more reasonable food con-

TABLE 3. Ecosystem indices for the Eastern Central Pacific ecosystem based on Trites et al. (*in press*). In the *Now* column, we present the starting point with present fishing pressure, while in *Then* we present a simulation modified with 10-fold increased biomasses of top predators and fishing excluded.

	Ecosystem attribute†	*Now*	*Then*	Trend‡
1	P_p/R	4.9	1.2	√
2	P_p/B	24	8	√
3	Biomass/energy throughput (%)	1.7	3.2	√
4	Net system production	700	142	√
6	Total consumer biomasses	18	103	√
12	Niche specialization	0.10	0.13	√
13	Average size (B/P)	0.04	0.09	√
15	Finn cycling index (%)	2	25	√
15	Path length	2.4	4.0	√
16	Average residence time (yr)	0.04	0.13	√
16	Trophic transfer efficiency (%)	12	16	√
17	Flow from detritus (%)	8	46	√
21	Utilization of detritus (%)	9	84	√
21	Utilization of P_p (%)	33	73	√
22	Schrödinger ratio (R/B)	5	7	√

† Numbers refer to attributes in Table 1. P_p is primary production, R system respiration, B system biomass, and P total production. See Christensen (1995) for a discussion of the attributes.

‡ "Trend" indicates accordance (√) with Odum's (1969) theory of ecosystem development.

version efficiency of 15%. Because of the increased production rate for the small pelagics, the biomasses of all consumer guilds except those of the top predators, were calculated using an assumed value of EE = 0.95, even for the reference (*Now*) model. The basic modeling approach was as described in the previous subsection with only the biomasses of the top predators (tuna, billfish, sharks, and dolphins) being increased in steps by 5, 10, 12.5, and up to 15 times (Table 4).

The system could not be balanced, even in 10 000 runs, with the top predator biomasses increased 15 times: the EEs (ecotrophic efficiencies indicating how large a proportion of the production is utilized in the system) would always exceed unity for the primary producers and detritus, i.e., more was used than produced of these groups.

A summary of ecosystem indices for the Gulf of Mexico models relevant to system maturity is presented in Table 5. As was the case for the Eastern Central Pacific simulation, the major result is a very clear trend for the indices to change in accordance with the predictions of Odum (1969), the only exception being the trophic transfer efficiencies which were lower in the simulation with increased top predator biomasses. This is because catches (in the *Now* model) were incorporated as part of the efficiencies.

The first two columns of numbers in Table 5 are quite similar, indicating that the ecosystem in its original state (the *Now* column) is in a configuration comparable to the case in which top predator biomasses were increased five-fold. In addition, the first two simulations show characteristics of immature systems sensu Odum (1969), notably little recycling of detritus. In contrast, the simulations with top predator in which biomasses

TABLE 4. System indices for the northern continental shelf of the Gulf of Mexico based on Browder (1993). *Now* is the starting point with present fishery; 5×, 10×, 12.5×, and 15× refer to modified models where the top predator biomasses are increased with the indicated factor and no catches are taken.

	Ecosystem attribute†	*Now*	5×	10×	12.5×	15×	Trend‡
1	P_p/R	7	12	1.3	1.1	0.8	√
2	P_p/B	70	88	20	17	14	√
3	Biomass/throughput (%)	0.6	0.5	1.6	1.8	2.0	√
4	Net system production	1053	1122	256	98	−184	√
6	Total consumer biomasses	9	6	54	63	79	√
12	Niche specialization	0.09	0.09	0.09	0.09	0.09	?
13	Average size (B/P)	0.01	0.01	0.04	0.04	0.05	√
15	Finn cycling index (%)	2	1	8	10	12	√
15	Path length	2.2	2.1	3.1	3.3	3.5	√
16	Average residence time (yr)	0.01	0.01	0.05	0.06	0.07	√
16	Transfer efficiency (%)	12.5	10.4	10.6	10.8	10.4	?
17	Flow from detritus (%)	10	5	32	37	37	√
21	Utilization of detritus (%)	11	5	70	88	132	√
21	Utilization of P_p (%)	9	7	68	74	105	√
22	Schrödinger ratio (R/B)	10	7	16	16	16	√

† See notes to Table 2.

‡ "Trend" indicates accordance (√) with Odum's (1969) theory of ecosystem development.

TABLE 5. Distribution of biomasses (g/m) by trophic level in the two trophic models of the Eastern Central Pacific. *Now* is the present-day model, while *Then* refers to the model where top predator biomasses are increased 10-fold.

Trophic level†	*Now*	*Then*
VI	0.003	0.03
V	0.07	0.7
IV	0.8	5.4
III	8	36
II	17	61

† Trophic levels are calculated based on diet compositions. Trophic level II encompasses herbivory and detritivory.

TABLE 6. Biomass distributions (g/m) by trophic level in the five versions of the Gulf of Mexico model. *Now* is the present-day model with catches, while 5×, 10×, 12.5×, and 15× refer to modified models where the top predator biomasses are increased with the indicated factor, and no catches are taken.

Trophic level	*Now*	5×	10×	12.5×	15×
V	0.02	0.01	0.12	0.14	0.16
IV	0.38	0.20	2.1	2.5	2.8
III	2.7	1.4	14	17	20
II	5.9	3.8	37	43	56

increased 10 or 15 times appear more mature sensu Odum. A clear indication of this is the biomass distribution by trophic level (Table 6): increasing the top predator biomasses seemed to require much higher biomasses on the lower consumer levels.

For the simulations carried out here, a major conclusion is that there is a striking correspondence between the behavior of Odum's attributes of ecosystem maturity and the ecosystem indices used here to quantify his attributes.

DISCUSSION

Open or closed systems?

Ecosystems do not operate in a vacuum: they are connected with their neighboring ecosystems and they undergo constant change. The acceptance of this has led to a new ecological paradigm in which the ecosystem is seen as an ''open system, one that is in a constant state of flux, usually without long-term stability, and affected by a series of human and other, often stochastic, factors, many originating outside of the ecosystem itself'' (Talbot 1996).

The open nature of ecosystems may, at first, seem to be a hindrance for mass-balance modeling of ecosystem flows. However, when ecosystems are properly defined so that the bulk of the trophic flows takes places between parts of the ecosystem, and this flow exceeds the flow between the ecosystem and its neighbors, and when the exchanges with the neighboring systems are quantified, the problem due to the open system nature of ecosystems is minimized.

Aquatic ecosystems need energy input in order to function. These can, however, be treated as import to the system. Therefore, there is no inherent problem with mass-balance modeling caused by the open nature of ecosystems.

Carrying capacity

In both of the simulations, it was possible to accommodate order-of-magnitude increases in top predator biomasses and the resulting large increases in overall consumer biomasses within the present levels of primary production. This should not be taken to mean that scenarios we simulate are realistic. If the top predator biomasses are increased by an order of magnitude in real life, we have no way of predicting the ecosystem consequences. What we say is that if there were that many top predators, the primary productivity might still be able to support it. Thus, our results only suggest that the ecosystems (as modeled) use primary production quite inefficiently in their present, exploited configurations. This should lead to increased accumulation of detritus in the sediments, and the eutrophication problems presently experienced in coastal systems throughout much of the world is in line with this.

We do not intend to suggest that ecosystem degradation due to fisheries is the sole or the main agent for this change; in many coastal areas eutrophication is certainly the dominant cause. Bu, we raise the possibility that fishery-induced ecosystem degradation may be a contributing factor.

Sedimentation is here implicitly quantified through two of Odum's attributes of maturity in Table 1: the ratio of gross primary production to total system respiration and the net community production, both defined by Odum (1969). In the mature ecosystem state, where net community production approaches unity, there is only limited sedimentation. As was shown in the Gulf of Mexico simulation, this is also the limit for how much the biomasses and, hence, the consumption in an ecosystem may increase: there has to be enough production to feed the consumers.

This limit can be interpreted as a functional definition of carrying capacity: the upper limit of biomass that can be supported by a set primary production and within a variable food web structure is reached when total system respiration equals the sum of primary production and detritus import.

Due to the variability allowed in the food web structure, some flexibility is possible. Still, there are limits: tunas will not start eating phytoplankton, nor will herring eat dolphins. We may then—at least in a simulation mode—apply this carrying capacity concept to any trophic ecosystem model to predict potential ecosystem configurations that both utilize the resources optimally and are thermodynamically possible.

The simulations

As shown in Tables 3 and 4, there is clear agreement between the present model simulations and key aspects of Odum's theory of ecosystem development. Questions remain, however. An important one is: is this trivial? In the present simulations, we increased the top predator biomasses by an order of magnitude while eliminating the human impact, i.e., the catches. Top-down driven models react to this by increasing biomasses at the prey levels. Since biomasses are an important part of Odum's theory, we do find that his attributes behave as expected.

However, biomass is just one of many factors considered by Odum's theory, and the biomass-independent attributes behaved as expected as well. Thus, we do view the results presented here as important because, while we used an approach derived independently from Odum's theory, they are in agreement with the basic tenet of that theory: that, given a primary production limited by external constraints, ecosystems may develop by internalizing flows and recycling detritus.

Indeed, most attributes of ecosystem maturity in Table 1 (e.g., the increased reticulation of food webs, or the retention of nutrients, or even species diversity) can be viewed as mechanisms by which recycling of detritus is increased.

Having simulated exploited ecosystems that can accommodate large increases in consumer biomasses with present levels of primary production, we may now ask how we should best manage ecosystems with overall biomasses as high as indicated in the present study (see Tables 5 and 6).

For the world's fisheries at large, overexploitation has resulted in degraded ecosystems that do not utilize their potential carrying capacity and that, therefore, lead to far less than optimal catch rates. We need to consider fisheries in a holistic ecosystem context to find a better way. By reducing or removing the large top predators and disrupting the retentive strands of the web of ecosystems, fishing may increase the detritus leakage from ecosystems. The overall productivity of exploited marine ecosystems is thus diminished, though we usually do not notice the loss because the human food supply is initially increased. The similarity between destructive fisheries and logging of old growth forests, whether temperate or tropical, will be appreciated.

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