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Toward a Stratified Mass-Balance Model of Trophic Fluxes in the Gulf of Mexico Large Marine Ecosystem

Daniel Pauly, Francisco Arreguín-Sánchez, Joan Browder, Villy Christensen, Sherry Manickchand-Heilemann, Eduardo Martinez, and Laura Vidal

Abstract

Construction of mass-balance trophic models of aquatic ecosystems, including complete food webs, from primary producers to top predators, is relatively straightforward. The resulting flow charts allow numerous inferences on ecosystems status and function and can serve as a basis for dynamic simulation models. Many applications of the Ecopath approach and software to lagoons, coastal systems, and other parts of the continental shelf of the Southern Gulf of Mexico (GOM) exist. Similar applications to various parts of the U.S. GOM coast, from Florida to Texas, are presently in preparation. A few models are available so far for the Northern Shelf system. We suggest a procedure in which these models, representing various subsystems of the GOM, are standardized and then linked to express the flows of biomass among them. Standardization of compartments will lead to a similar treatment, in the Mexican and U.S. sectors of the GOM, of fisheries catch data (including discarded bycatch), and of marine mammals, turtles, and other sensitive groups. Expected outputs are listed, and some preliminary results are presented, based on the Ecopath models constructed to date.

The Gulf of Mexico (GOM) is, at 1,623,000 km², the largest semienclosed coastal sea of the western Atlantic and, although large, meets the criteria used to define a large marine ecosystem (LME; see e.g. contributions in Sherman and Alexander 1989). Also, its internal fluxes are sufficiently strong, relative to fluxes into and out of the GOM, for its elements to form an integrated ecosystem rather than an assemblage of independent parts (see Chap. 4).

Although it is straightforward, when describing its gross attributes, to establish the ecosystem nature of the GOM, it is another thing to follow-up

on the local implications of such diagnosis, that is, to quantify the transfers within and among the various subsystems of the GOM.

This contribution outlines a strategy, patterned after that in Pauly and Christensen (1993), for constructing stratified mass-balance models of trophic fluxes in the GOM. Note that a stratification is required for two interrelated reasons: to allow incorporation into component submodels of as much local data as possible on trophic groups and interactions occurring in distinct subsystems of the GOM and to account for spatial differences in flux structure and amplitudes.

The model will use *mass balance* as its structuring element because this approach has so far proven invaluable for ecosystem modeling, notably by forcing realistic solutions even in data-sparse situations and by allowing identification of mutually incompatible estimates of various rates (see e.g. contributions in Christensen and Pauly 1993).

The model, finally, will deal with *trophic fluxes* because feeding and being fed on strongly link different groups of organisms and because other non-feeding interactions do not seem suitable for modeling the upper trophic levels of marine ecosystems. Thus, for example, physical forcing of nutrient inputs can often explain fluctuation of primary production, without considering grazing by herbivores. However, this cannot lead to prediction of fisheries yields, which tend to be mediated by trophic interactions among higher trophic levels (see contributions in Daan and Sissenwine 1991).

Ecopath Approach for Mass-Balance Modeling

The Ecopath approach and software for constructing mass-balance trophic models of ecosystems has been widely used in the GOM, and thus detailed descriptions of subsystems of the GOM exist (Table 17-1, Fig 17-1). For any (sub)system, this consists of solving the system of linear equations:

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum B_j \cdot (Q/B)_j \cdot DC_{ij} \quad (1)$$

where B_i and B_j are the biomasses of functional groups of preys and predators (or food items and their consumers), respectively; P/B_i the production/biomass ratio of group i , equivalent to its mortality rate (Allen 1971); EE_i its ecotrophic efficiency, or the fraction of its biologic production ($P_i = (B_i \cdot (P/B)_i)$) that is consumed within the system in Eq. (1); Y_i the fisheries yield of i (if any); whereas the summation sign adds up all sources of predation on i , caused by predators (or grazers) j ; Q/B_j is the food consumption (i.e., food requirements of j); and DC_{ij} the fraction of i in the diet of j .

The equations in Eq. (1) are easy to parameterize for most systems because numerous estimates of B , P/B , Q/B , Y , and diet composition are available in

Table 17-1. Existing and forthcoming mass-balance trophic models of the Gulf of Mexico

(sub)System	No. in Figure 17-1	Remarks	Reference
Southern GOM, Mexico^a			
Western GOM	1	Shrimping grounds; model to consider discarded bycatch	In preparation ^a
Tamiahua Lagoon	2	Update to include fisheries catches	Abarca-Arenas and Valero-Pacheco (1993)
Tampamachoco Lagoon	3	Update to include fisheries catches	Rosado and Guzman del Proo (in prep.) ^a
Southwestern GOM	4	Parameterized using trawl surveys data	Arreguín-Sánchez et al. (1993a) de la Cruz-Aguero (1993)
Mandinga Lagoon	5	Update to consider horizontal coupling with shelf	Pauly et al. (1994)
Terminos Lagoon	6a	Very preliminary model, to be updated ^a	Rivera-Arriaga et al. (1998)
Terminos Lagoon	6b	Mangrove/seagrass subsystem	Manickchand-Heileman et al. (1998)
Campeche Sound	7a	Parameterized using trawl surveys data for 1988–1994; model is illustrated in Fig 17-2	
Campeche Sound	8b	Coastal waters (beach seine fishery)	Vega-Cendejas et al. (1993)
Celestun Lagoon	9a	Update, in Arreguín-Sánchez et al. (1998), will include fisheries catches and birds	Chávez et al. (1993)
Celestun Lagoon	9b	Model of mangrove subsystem	Vega-Cendejas (1998)
Alacranes Reef	10	To be based, in part, on Opitz (1996; see also Figs 17-4 and 17-5)	In preparation ^a
Yucatan Shelf	11	Emphasis on exploited species	Arreguín-Sánchez et al. (1993b)
Northern GOM, USA^b			
Looe Key Reef, Florida	12	Coral reef system; Venier (MSc thesis, in prep.) emphasize changes through four seasons, each with its own model	Venier and Pauly (1997)
St. Marks National Wildlife Refuge, Florida	13	Winter model, emphasizing birds; a summer model is also available from the same authors	Christian and Luczkovich (1996)
Florida to Texas shelf	14	To be updated with emphasis on fisheries bycatches; see also Figs 17-4 and 17-5	Browder (1993); update in Arreguín-Sánchez et al. (1998)
Galveston Bay Estuary	15	To be based on McFarlane (1993)	Martinez and McFarlane (in prep.) ^b
Entire GOM^c			
Offshore areas	16	Model for waters > 200 m, with couplings to shelf models	In preparation ^c
Entire GOM	—	Integration of all available models, as described in this contribution; may also include submodel for Cuban waters.	In preparation ^c

^aFor more information, contact F. Arreguín-Sánchez and/or S. Manickchand-Heileman.

^bFor more information, contact J. Browder and/or E. Martinez.

^cFor more information, contact D. Pauly, V. Christensen, and/or L. Vidal.

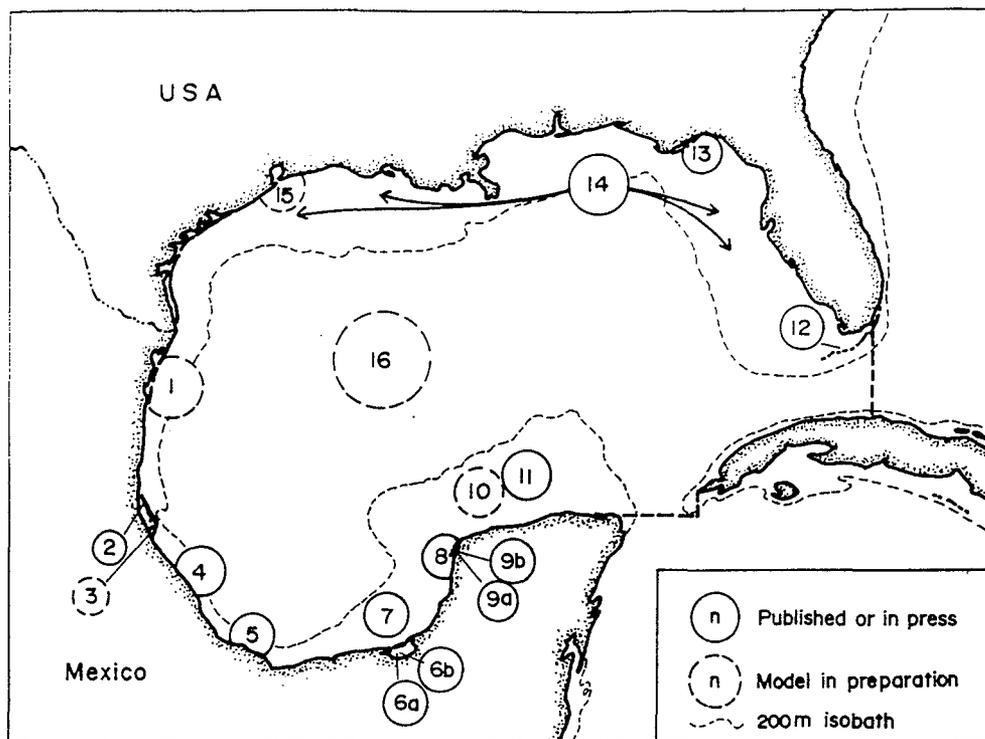


Figure 17-1. Areas represented by published or forthcoming mass-balance trophic models of subsystems of the GOM LME (see Table 17-1 for details on models 1–15). Note predominance of published models in the Mexican half of the GOM to be matched by new Ecopath models from the U.S. coast.

the literature, a result of traditional single-species studies by fisheries scientists and marine biologists (see e.g. Richards and McGowan 1989) or the FishBase CD-ROM (Froese and Pauly 1998). Combining these published estimates with original data is straightforward and allows estimation of the EE_n , which defines the fluxes among (sub)systems. Indeed, such combinations of estimations, which can also be done in a Bayesian context that considers the uncertainties associated with these estimates (Walters 1996), can be seen as a form of validation, because they generate data sets that are mutually compatible under mass-balance constraints (Christensen and Pauly 1992a, 1995). This is the case for the models of areas of the GOM constructed so far (Table 17-1), which all describe thermodynamically “possible” systems, of which Figure 17-2 is an example. However, these models emphasize different aspects of the subsystems they describe, and leave significant gaps in their coverage of the GOM as a whole (Fig 17-1).

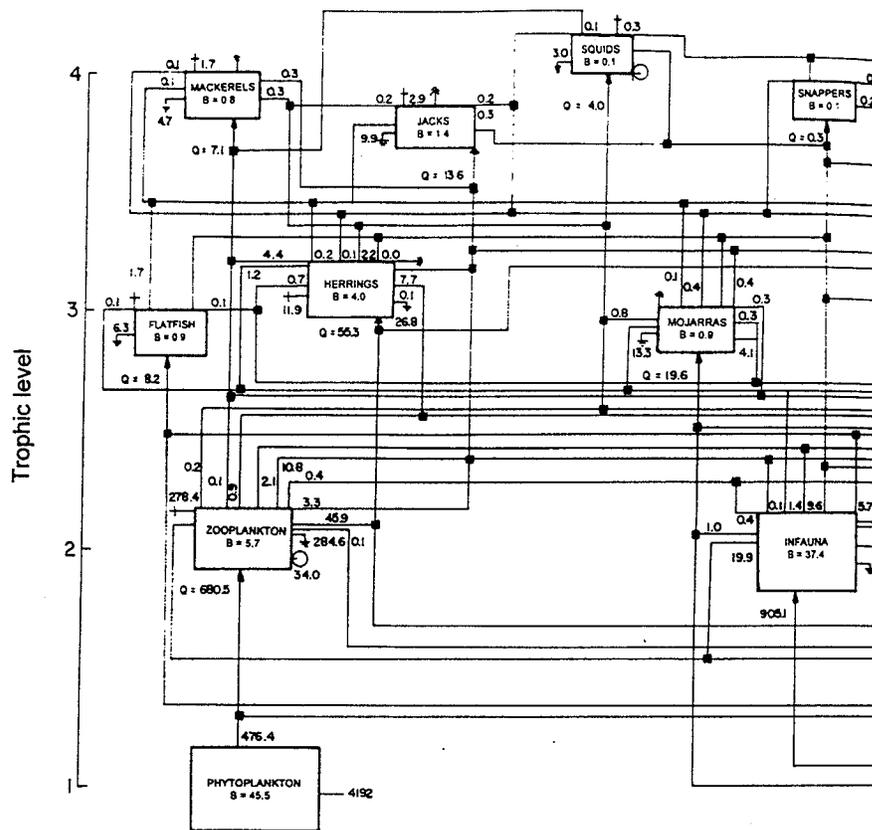


Figure 17-2. Example of a mass-balance trophic model from Campeche Sound, southwestern GOM, based on trawl survey and other local data (Manickchand-Heileman et al., unpublished data). In this representation, the size of the boxes is roughly proportional to the logarithm of the biomasses (in t wet weight/km²); the consumption flows (t wet weight/km²/yr) are shown, but the respiratory flows and the backflows to the detritus are omitted for clarity.

Need for Standardization and Stratification

To address these inconsistencies, our strategy must include steps leading to (a) a standardization of functional groups [items i and j in Eq. (1)] included in the models and (b) a stratification scheme wherein the existing and forthcoming Ecopath models are made to represent parts of the GOM that add up to the entire system. Item (a) is addressed by modifying existing and forthcoming models according to the following criteria:

1. All models must include fisheries catches for their area such that the sum of all catches, for all areas, adds up to the total reported fishery catches of the entire GOM;

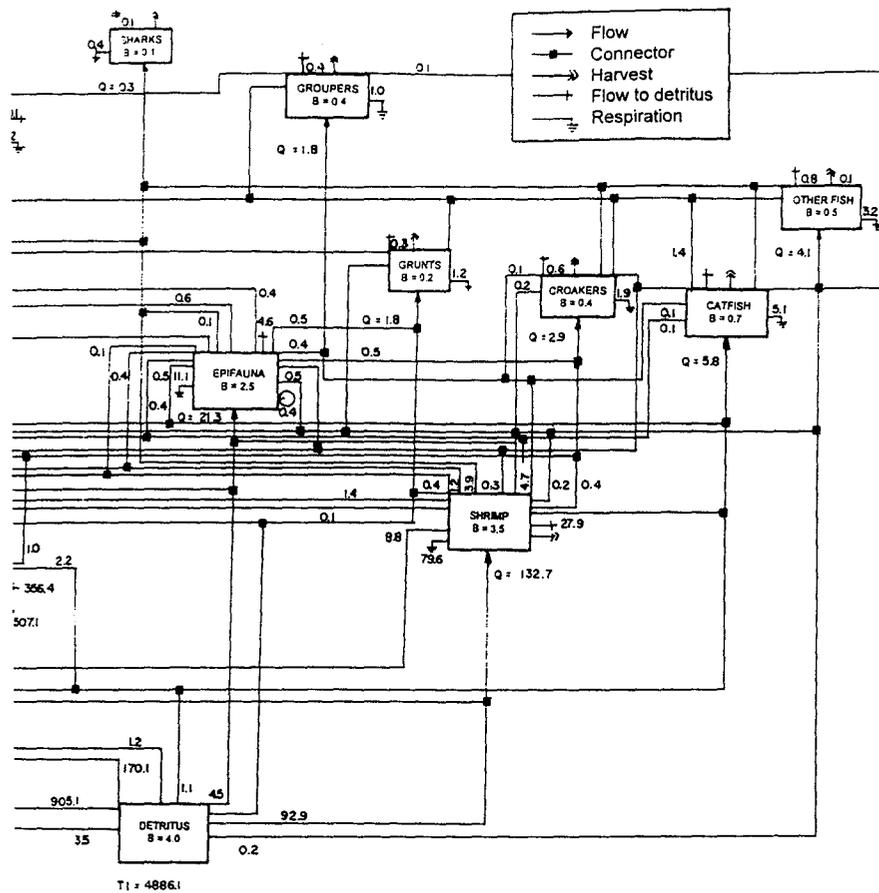


Figure 17-2. Continued.

- Models must include marine mammals (by functional groups), seabirds, and turtles such that their combined populations, for the entire GOM, approximates the best available independent estimates;
- Lagoon, estuarine, and inshore models should include among their functional groups mainly the juveniles of species with strong ontogenic offshore migration and shifts in diet composition, whereas the shelf and offshore models should include mainly the adult forms.

This last point is important in that it will allow quantifying the role of lagoons, estuaries, and other coastal water bodies as sources of recruits to the populations, using a dynamic simulation model called Ecosim, derived from Ecopath, that includes a representation of ontogenic shifts (Walters et al. 1997).

Presently, the Ecopath software is designed to accommodate up to 50 functional groups, and only two applications were detailed enough to reach this

upper limit (Arias-Gonzalez 1993; Opitz 1996). Given its stratified nature, we anticipate the model described here to exceed this limit by at least a factor of 10. This will either require a modification of the software, allowing it to invert very large matrices, for example, as done in community studies (De la Cruz 1994); or using Ecospace, a recently developed software (Walters et al. 1998) as an integrative tool.

Standardization of fisheries catches is important, because such catches, when accurate, can be used to compute the biomasses of fishes of higher trophic levels, which are otherwise difficult to estimate. Accurate catches consist of *nominal catches* (i.e., catches reported in official fisheries statistics) (reviewed in Richards and McGowan 1989), illegal and unreported catches (often large, in both recreational and commercial fisheries), and discarded bycatch (a large component of the GOM trawl fisheries). Further, the fate of the discarded bycatch must be specified. This can be done, in the Ecopath context, by identifying the groups that feed on discarded bycatch (e.g., birds and sharks near the surface and crabs at the bottom), as suggested by Hill and Wassenberg (1990) and Wassenberg and Hill (1990).

Considering marine mammals when constructing trophic models is straightforward, as a standardized compilation now exists of the diet composition of all their species (Pauly et al. 1995). Given suitable local data, these global means can easily be adjusted to GOM conditions. Feeding and mortality rates and population estimates also exist for turtles, seabirds, and other sensitive groups (see e.g. contributions in Christensen and Pauly 1993), and thus their incorporation into trophic models poses no problems as far as parameter estimation is concerned.

Addressing item (b) above involves breaking up the GOM into relatively homogenous strata, most probably defined by depth (0–10, 10–20, 20–50, 50–100, and 100–200 m and off shelf) and by states (of Mexico and the United States) while accounting for key coastal systems (e.g., the mouth of the Mississippi in the United States, Terminos Lagoon in Mexico, and coral reef systems throughout the GOM). Because the distribution of published models is very uneven between the United States and Mexico (Table 17-1), more collaborators willing to model subsystems of the northern GOM will have to be identified.

Expected and Preliminary Results

The Ecopath approach, in a strange contrast to the GIGO phenomenon (Garbage In, Garbage Out), can be described in terms of MIMO (i.e., Minimum In, Maximum Out). Indeed, the data required to parameterize the system of equations in Eq. (1) can be viewed as the minimum input that can

be expected of a would-be ecosystem modeler. On the other hand, the outputs, and thus insights, that can be derived from quantified food webs such as generated by Eq. (1) are so numerous that they cannot be listed in a brief document such as this. A selected list includes:

1. Trophic levels (and their variance, an index of omnivory) for all groups in each (sub)system;
2. Estimation of biomass, consumption, respiration, and so on by trophic levels, as required to construct and compare trophic pyramids (Fig 17-3);
3. Most elements of Odum's theory of ecosystem development (Odum 1969), some previously not quantifiable;
4. All elements of Ulanowicz' theory of ecosystem phenomenology (Ulanowicz 1986).

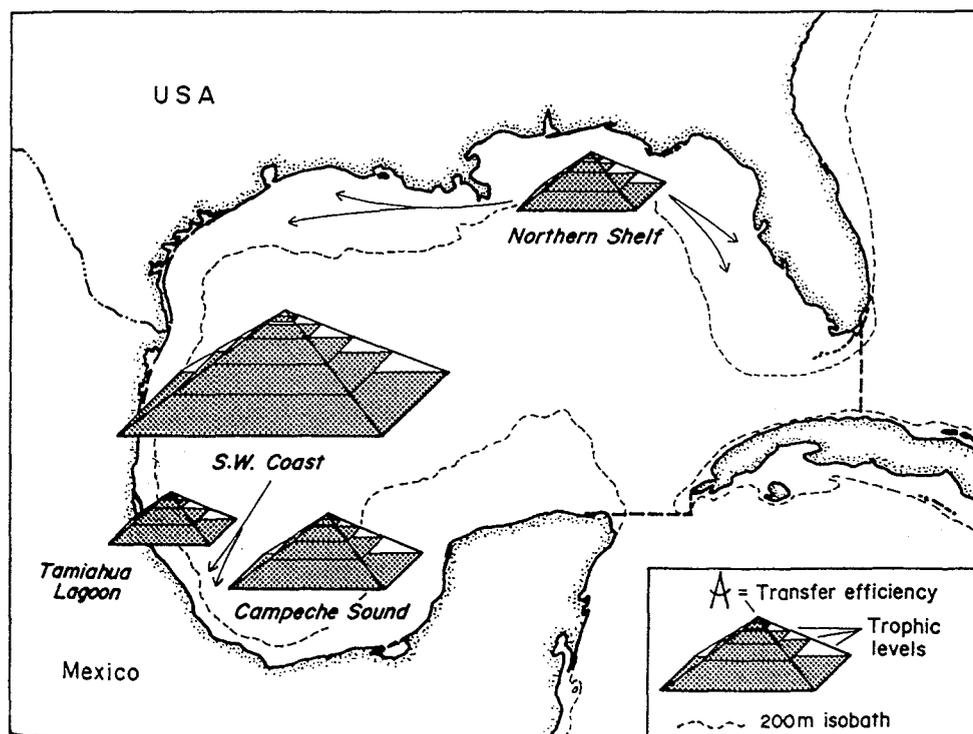


Figure 17-3. Trophic pyramids of four selected subsystems of the GOM LME as output by Ecopath. The volume of these pyramids at any trophic level is proportional to the trophic fluxes at that level, whereas the top angle is (inversely) proportional to the mean transfer efficiency between trophic level. Hence, pointed pyramids, which imply a high transfer efficiency, will tend to have numerous trophic levels and conversely for pyramids with obtuse top angles. The comparison here suggests similar efficiencies in all subsystems but vastly different amount of fluxes, mainly due to differences in primary production and detritus inputs and to the amount of recycling.

Applications discussing these and related properties of ecosystems modeled using Ecopath may be found in Christensen and Pauly (1992a, 1992b, 1995, 1996, 1998), Pauly and Christensen (1993, 1995), and contributions in Christensen and Pauly (1993), notably by Arreguín-Sánchez and collaborators (Vega-Cendejas et al. 1993; Arreguín-Sánchez et al. 1993a, 1993b).

The stratified model of the GOM that will result from the work outlined above will also generate the variety of results in 1 to 4 and more and should thus "feed" into numerous initiatives devoted to understanding the functioning of the GOM as an LME. This may be illustrated by two examples.

The first example is based on one of the GOM subsystem models published so far (Browder 1993), representing the northern shelf of the GOM and which is here compared with a model representing an unexploited coral reef system (Opitz 1993). This example is meant to illustrate the potential use of Ecopath models in reaching a functional definition of "carrying capacity," a concept that has so far remained elusive, at least as far as LMEs are concerned.

Ecopath can estimate the parameters of the system of linear Eq. (1) from the top down. Thus, by increasing the input biomasses of top predators, while maintaining primary production at its original value, Ecopath can be forced to find solutions to Eq. (1) that increase prey biomasses, to maintain mass-balance, while more fully utilizing primary production (Christensen and Pauly 1998).

This approach was implemented through the Ecoranger routine of Ecopath, which allows entering normal, triangular, or uniform distributions (i.e., ranges) about inputs to Eq. (1) and then resamples these distributions in Monte Carlo fashion, using the sampled inputs to generate a large number of random models. Of these, most fail to meet mass-balance and other consistency criteria, leaving a reduced number of "possible" models to generate output distributions that can be interpreted in a Bayesian context (Walters 1996) and/or in terms of a prior hypothesis. Figure 17-4 and Table 17-2 summarize the results obtained here.

As might be seen, for the model representing an unexploited Virgin Island reef, top predator biomass could be increased by a factor of 4 and total biomass by a factor of 2 before the fraction of "possible" realization dropped below 50% and beyond, and thus reached carrying capacity as defined here. To achieve the same for the GOM, predator biomass had to be increased about 15 times and total biomass 5 times. That the Virgin Island reefs, as an unexploited system, had a total biomass of about one half carrying capacity may be a generic feature of unexploited systems. (This is obviously a question to be studied further.) If so, this would imply that the GOM shelf system analyzed here, with a biomass of one fifth carrying capacity, could, if rehabilitated, accommodate a biomass two to three times larger than at present.

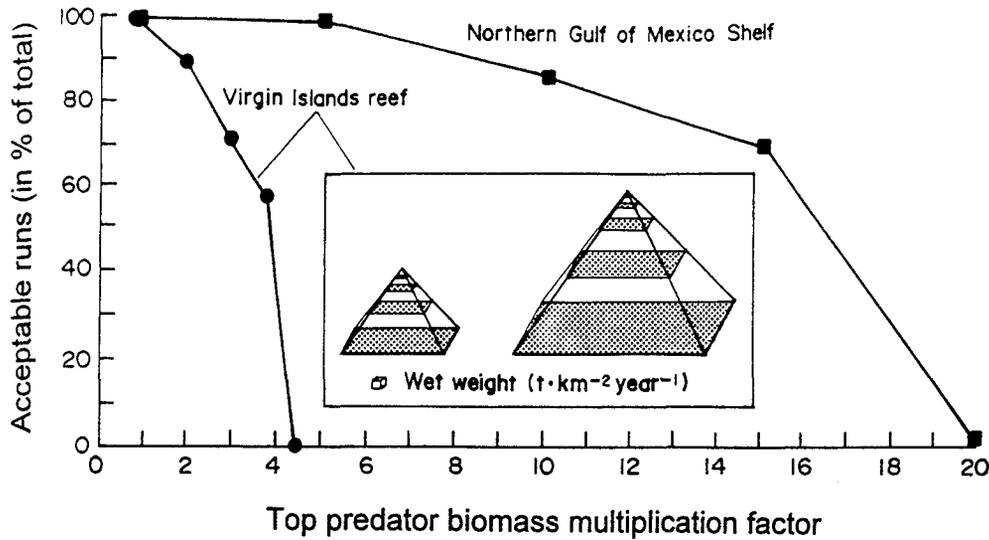


Figure 17-4. Effect on Ecopath models of multiplying top predator biomass by a fixed value and then letting a Monte Carlo routine select the best set of input parameters from uniform distributions ranging 20% on either side of the original inputs: biomass (B), food consumption (Q/B), production rate (P/B), and diet composition (DC) (see Christensen and Pauly 1998); Note that the unexploited system (Virgin Island reef; inset) was nearer carrying capacity (i.e., value of factor where accepted runs drop below 50%) than the exploited GOM (see Table 17-2).

Table 17-2. Output of Ecopath simulation wherein the models representing (unexploited) Virgin Island coral reefs and the (exploited) Northern Gulf of Mexico shelf were imposed a higher biomass of predators, forcing an increase in overall system biomass

System Property	Virgin Islands		Gulf of Mexico	
	OR	CC	OR	CC
Biomass multipl. factor ^a	1	4	1	15
Total biomass (t/km ²) ^b	2,100	4,400	13	67
Biomass change (%)	209		515	
Finn's cycling index	4.7	14	2.7	8.3
System B/P^c	0.9	0.16	0.1	0.4

Results are given for two states: original levels of biomass (OR) and after biomass increases, i. e., near carrying capacity (CC); see also Figure 17-4 and Christensen and Pauly (1998).

^aFor top predators only.

^bIncrease of total biomass was generated from the top down, through the food requirements of the top predators.

^cAn index of maturity whose inverse (system P/B) indicates that systems near CC have, overall, a lower turnover than developing systems (Odum 1969).

We note further, in Figure 17-5, that given constant primary production levels, increased biomasses can be accommodated in both systems only by increasing recycling of detritus (i.e., by increasing the detritus component of the diet of various consumers). (In the simulations described above, the diet

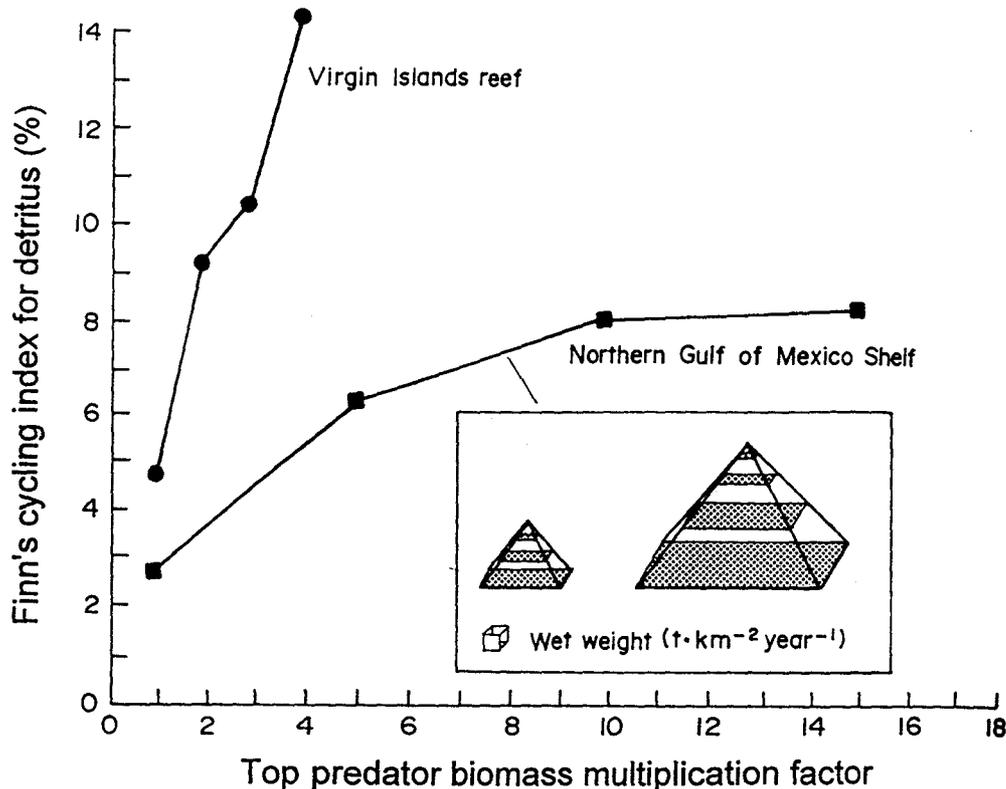


Figure 17-5. Relationship in two ecosystem models between Finn's cycling index (expressing the percentage of detritus that is recycled *within*, relative to the amount flowing *through* the system) and top predator biomass increases as used to force, from the top down, an overall increase of system biomass. This simulation shows that, given constant primary production, it is the amount of detritus recycling that determines the size of a system (i.e., its carrying capacity). The northern GOM shelf (inset) could thus carry a much higher biomass than it presently does (see Table 17-2).

compositions of the various functional groups included in the models are also made to vary randomly, i.e., may include a larger fraction of detritus than was incorporated in the original model.)

Conversely, this implies that depleting through fishing the diversity and the biomass of consumers may decrease the fraction of detritus used (i.e., respired) within the food web and thus may lead to increased detritus accumulation on the sea bottom (Christensen and Pauly 1996; see also Browder 1983; Walsh 1983). This effect will tend to exacerbate the O_2 depletion problem reported from the Louisiana-Texas shelf (Rabalais et al. 1994, 1996).

Our other related example of Ecopath applications leading to increasing understanding of an LME is provided by the estimation of the primary production required (PPR) to sustain fisheries, which can be determined, given a

Table 17-3. Estimation of the primary production required by the Mexican Atlantic shelf fisheries (GOM and Caribbean Coast)

Item	Estimate (units)
Shelf area (0–200 m)	2,500 (10 ³ /km ²)
Primary production	310 ^a (gC/m ² /y)
Shelf primary production	76.5 (tC/10 ⁶ /y)
PP required by fisheries	26.3 (% of PP) ^b

^aMean for tropical shelves in Pauly and Christensen (1995); Table 17-1 in Longhurst et al. (1995) gives a lower value (190 tC/10⁶/y) for the area covered here.

^bNot accounting for discarded bycatch (see text) nor for the lower primary production in "a" above.

knowledge of fisheries catches, from the trophic levels (TL) of the exploited groups represented in those catches, and the transfer efficiency between TLs, two outputs of Ecopath (Christensen and Pauly 1992; Pauly and Christensen 1995) (Fig 17-2). The key equation here is

$$PPR = (\text{Fisheries catches} \div 9) \cdot 10^{\text{TL}-1} \quad (2)$$

where 9 is the ratio of carbon, commonly used to quantify primary production, to wet weight, used to quantify fisheries catches and the term $10^{\text{TL}-1}$ is based on the mean transfer efficiency of 10% estimated by Pauly and Christensen (1995) from 48 Ecopath models, describing aquatic ecosystems throughout the world.

Pending the integrated GOM model described above, we have applied Eq. (2) to all major fisheries groups in catch statistics from the Atlantic coast of Mexico (mainly GOM but also including catches from its Caribbean Coast). This led to the results summarized in Table 17-3. As might be seen, the estimated PPR represents one quarter of observed primary production, the rest being required by marine mammals, birds, and other top predators or ending up as part of the detritus (see above). Although within the range of values for tropical shelves (Pauly and Christensen 1995), this PPR estimate may be on the low side because it does not account for the large amount of discarded bycatch of the shrimp fisheries (Alverson et al. 1994). On the other hand, the primary production value used for this second example may be too low. Hence, the stratified model proposed here will enable analyses requiring accurate estimates of primary production for the GOM as a whole.

Conclusions

A methodology exists with which the key trophic interactions in LMEs can be described and quantified, and we propose to apply it to the GOM. These results

will be more useful the smaller the scale that is used for the spatial stratification of the overall model. Also, more "local" models will mean more consideration of local data and constraints and hence a more realistic overall model and more realistic aggregate statistics (e.g., such as the PPR to sustain the fisheries of the GOM). We thus invite colleagues interested in doing so to collaborate with us on this project on the basis of our common interest in the GOM as an LME.

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