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# Integration of subsystems models as a tool toward describing feeding interactions and fisheries impacts in a large marine ecosystem, the Gulf of Mexico

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## Abstract

This contribution documents, using the example of the Gulf of Mexico large marine ecosystem (GoM) LME, how mass-balance, trophic ('Ecopath') models can be synthesized into a single integrated, spatially explicit model, from which various inferences on the ecological functioning of, and fisheries impacts on an LME can be drawn. The 10 component models used here covered inshore subsystems (lagoon, coral reefs), shelves, the open waters of the GoM, both in Mexican and US waters, and the GoMs Central Gyre, and were integrated using the Ecopath with Ecosim software. The main features of the synthetic trophic model resulting from this integration are presented, along with several time dynamic (Ecosim) and spatial simulations (Ecospace). Jointly, their results suggest the GoM to be rather robust as a whole, although continued increases in fishing effort, especially by bottom (shrimp) trawlers, will have serious impacts, reverberating through the entire shelf subsystem.

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## 1. Introduction

Fisheries are in crisis worldwide, while their impacts upon the ecosystems in which they are embedded are increasingly being seen as the major force impacting change by affecting productivity, and even continued existence [1,2]. Overcoming this crisis implies a change in the manner fisheries are managed. The term ‘fisheries management’ so far generally implies managing the fleet targeting a (specific set of) species, generally without explicit reference to other species that are affected, or even caught by that fishery (the by-catch), nor to the ecosystem supporting these species.

‘Ecosystem-based fisheries management’ (EBFM) has been proposed as an alternative approach [3], with ‘ecosystem management’ as the ultimate goal, i.e., a form of management that would consider not only fisheries, but other concurrent ocean uses, e.g., through zoning [2]. However, whether or not EBFM is intended, any departure from single-species management requires models explicitly accounting for the biological, especially trophic interactions, between ecosystem components.

This is one of the reasons, given widespread interest in a transition towards EBFM, for the construction of the trophic model of ecosystems by fisheries scientists, an activity that has led to many pertinent publications in the last decade (see contributions in [4] and [www.ecopath.org](http://www.ecopath.org)). Most of these trophic models were constructed, in the form of mass-balanced food web, using early versions of what is now the Ecopath with Ecosim (EwE) software [5,6], and generally cover small subsets of Large Marine Ecosystems (LME) sensu [7,8]. Here, we show how a number of such local models can be synthesized into a single, integrated LME-scale model, and used to draw various inferences on the functioning of that LME, and the impact that fisheries have on its structure and productivity.

## 2. Modelling large marine ecosystems

Before the ascent of mass-balance trophic (‘Ecopath’) models, only few attempts had been made to model entire LMEs. The most influential among these attempts was the North Sea model of [9], which used nearly six hundred differential equations to track individual numbers in 20 populations of commercial fishes, their prey biomass, and which explicitly described primary and secondary production, and predators’ prey selection, growth and reproduction processes. This model was never duplicated outside the laboratory where it was created, but it nevertheless had a huge impact on the development of Multispecies Virtual Analysis (MSVPA) [10], both by demonstrating the feasibility of modelling an entire LME (though not in spatially explicit fashion), and through its representation of various processes (notably size-selective prey selection), which MSVP took over. However, MSVP itself, though a simplification of the Andersen and Ursin model, still had exceedingly high data requirements, and has been applied in only few areas outside of the North Sea (Baltic Sea, Eastern Bering Sea).

Another influential approach toward LME modelling was the work documented in [11], wherein the biomass and food requirements of marine mammals were

combined with spatially disaggregated fisheries catch data to simulate biomass fluxes between spatial cells representing the North Pacific LME. Perhaps the major impact this model had was to inspire [12] to develop the Ecopath approach and software which he presented as a version of the model [11], stripped of its temporal and spatial dimensions. Thus, Ecopath models represent only the biomasses of functional groups, and the fluxes between them as a ‘snapshot,’ representing a given period in time [5].

The ease with which Ecopath models can be constructed, notably from data extracted via a specially programmed change by pre-programmed routine of FishBase [13], has led to nearly 200 such models being published, many covering parts of various LMEs (see [www.ecopath.org](http://www.ecopath.org)). Thus, it became possible to consider the integration of such models into synthetic models of entire LMEs. Here, two approaches can be taken. The first is to link the export flows of a set of models representing different parts of an LME with the corresponding imports, leading to mass balance for the set as a whole. This approach was applied by [14] to 10 models representing subsystems of the South China Sea, linked by the (offshore) transfer of detritus. This allowed, e.g., the estimation of a net detritus outflow to the deeper, central part of the South China Sea.

The other approach, documented here, is to combine component models into a single Ecopath model of an LME, as described for the Gulf of Mexico (GoM) by [15] in a contribution which prepared for the work presented here. This then allows parameterization of the time-explicit module of EwE, Ecosim [16], and of its spatial counterpart, Ecospace [17], both duplicating, although in much more traceable fashion, functions of the models of [9,11]. We reiterate below the main features of this approach, with emphasis on its spatially explicit element, following a brief description of the GoM LME.

### 3. The Gulf of Mexico as a large marine ecosystem

The GoM is located between tropical and subtropical North Atlantic latitudes, and includes a wide variety of marine habitats. As one of the 64 LMEs defined by [7,8], generating the overwhelming bulk of the world’s fisheries catch (see <http://saup.fisheries.ubc.ca/lme/lme.asp>), the GoM is one of the economically most important water bodies within the Mexican and US Exclusive Economic Zones. With a surface area of 1623 km<sup>2</sup> when defined as in Fig. 1, the GoM now supports fishery landings of over one million tonnes per year (Fig. 2), not accounting for a large amount of discards (see below). However, in the last decades, commercial and recreational pressures (fisheries, tourism, marine shipping, mineral extraction, oil and gas extraction) on the GoM have increased, particularly along coastlines. Many fish stocks show evident symptoms of overexploitation, resulting in catch declines since the peak of the early 1980s (Fig. 2) and coastal habitats have been severely damaged, e.g. the enormous wetland loss in the Mississippi delta [18]. Indeed, the GoM now suffers every summer from large and growing ‘dead zones,’ where lack of dissolved oxygen induces widespread mortalities [19]. However, no plan for the management of the GoM as a whole appears to exist, and integrative studies are still

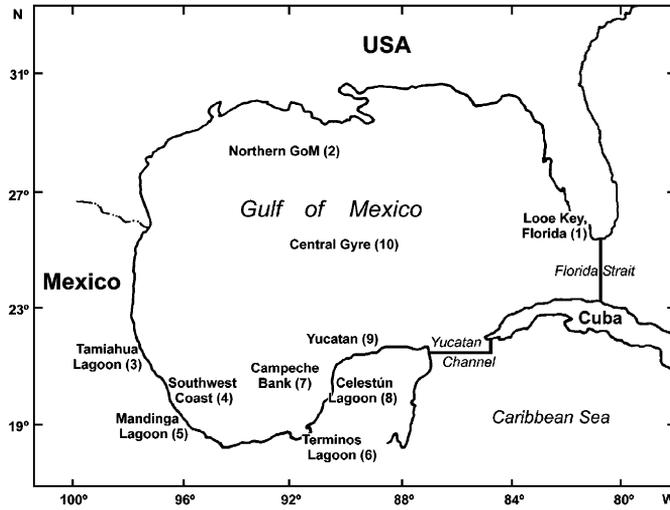


Fig. 1. Limits of the GoMLME as used in this contribution, with names indicating the local models incorporated in the synthetic model of the entire Gulf (see also Table 2).

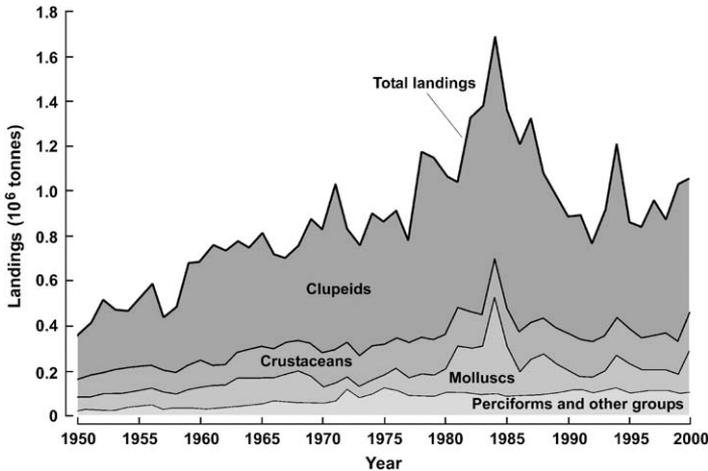


Fig. 2. Trends in fisheries landings from the GoM, as defined in Fig. 1, based on Mexican, US, and FAO data. Note decline since the early 1980s, largely due to excessive fishing effort. Also note that these landings represent, at least for the late 1980s/early 1990s, only 44% of the total catch, the other 56 consisting of discarded by-catch, mainly by bottom trawlers (see text).

scarce, e.g. [20] suggested a management plan for the entire Mississippi basin to remove nitrogen from the river, in spite of volumes being devoted to its biology and exploitation, see e.g. contributions in [21].

Table 1 lists major subsystems of the GoM, and their contribution to the whole. Note that these subsystems are embedded in distinct depth strata, viz: (a) coastal

Table 1  
Subsystem of the GoM LME

Subsystem	Depth (m)	Area (10 <sup>3</sup> km <sup>2</sup> )
Estuaries	0–20	34
Shallow non-estuarine, non-reefs	0–20	119
Coral reefs	10–50	2
Soft bottoms	20–200	441
Open ocean	>200	1026
Total	0–3400	1623

shallows from 0 to 20 m (152,600 km<sup>2</sup>); (b) continental shelf from 20 to 200 m (443,800 km<sup>2</sup>); and (c) oceanic waters with depth >200 m (1,026,500 km<sup>2</sup>). The coastal shallows were further subdivided, where appropriate, into: (i) estuarine, (ii) coral reefs, and (iii) non-estuarine/non reef areas (Table 1). The continental shelf was assumed to consist only of soft bottom, i.e., to be trawlable throughout.

#### 4. Material and methods

The methodology used for this contribution follows [22–24] and consists of the following steps:

- (1) identification of area and period to be covered;
- (2) definition and parameterization of ecosystem functional groups;
- (3) model balancing and verification;
- (4) analysis of model features and behaviour (i.e., policy exploration).

Step 1 led to the identification of the following geographical limits: from Cabo Catoche in Yucatan to Punta Perpetua on the Western end of Cuba, and from Bahia Santa Clara, in Northwestern Cuba to Long Sound in Florida Bay (Fig. 1). The estimation of the area of the GoM, in total and by subsystem, was done using a digitized map of the US Geological Survey with a scale of 1:2,750,000. Areas for US and Mexico waters shallower than 200 m were determined at 10, 50 and 100 m from digitized topographic maps produced by the US Geological Survey and the Mexican Ministry of Defence. For Cuba, this information was not readily available, and relative proportions from the other two countries were used.

The 10 trophic mass-balance (Ecopath) models used here are summarized in Table 2. There are less than the 16 models in Table 17-1 of [15], which included models then ‘in preparation’ but which were not available when this study was performed. Given the periods covered by these local models, the synthetic model of the GoM presented here provides a snapshot of the late 1980s to the early 1990s.

Step 2 involved identifying functional groups which would represent a compromise between the need for parsimony vs. the need to consider the many distinct groups included in the local models, to represent major ecosystem types, and

Table 2

Local models incorporated in the synthetic mass-balance trophic model of the GoM LME

Model (US/Mexico)	# of groups	# in Fig. 1	System type	GoM area <sup>a</sup> (10 <sup>3</sup> km <sup>2</sup> )	Sources and remarks <sup>b,c</sup>
Looe Key, Florida (US)	18	1	Coral reef	2.5	[36,37]
Northern GoM (US)	15	2	Soft bottom shelf	253.8	[38]
Tamiahua Lagoon (M)	13	3	Estuary	11.8	[39]
Southwest coast (M)	19	4	Non-estuarine, non-reef	118.6	[40] Based mainly on trawl survey data
Mandinga Lagoon (M)	20	5	Estuary	11.8	[41]
Terminos Lagoon (M)	20	6	Estuary	2.0	[42]
Campeche Bank (M)	19	7	Soft bottom shelf	93.7	[43]
Celestún Lagoon (M)	16	8	Estuary	8.3	[44]
Yucatan (M)	21	9	Soft bottom shelf	93.7	[45]
Central GoM	10	10	Central Gyre	1026.6	Modified from central south China Sea model of [14], itself based, in part, on data from the GoM

<sup>a</sup>Scaling from area covered by model to entire GoM based on provinces defined in [46].

<sup>b</sup>Other models of parts of the GoM exist [47,48] but they were not included as the files documenting them were not available to the authors.

<sup>c</sup>Fisheries landings and discards were added independently to those values reported in the original models.

to consider important top predators such as seabirds and marine mammals, often ignored in local models. This led to a compromise of 40 functional groups: three primary producers (benthic producers: inshore phytoplankton, offshore phytoplankton); two non-living groups (detritus and discards); eight herbivores and/or detritivores (mainly invertebrates, including planktonic and benthic forms, the latter ranging from meio- to macrobenthos), and 29 other consumers, including turtles, seabirds and two marine mammal groups.

The 597 species of fish occurring in the GoM (see [www.fishbase.org](http://www.fishbase.org)) were first split into four habitat types (coastal, reef, shelf or oceanic), habits (demersal or pelagic) and size (small < 30 cm [total length]; medium 30–60 cm; large > 60 cm; except for coral reef fishes where small < 20 cm and large > 20 cm), feeding type (planktivory/herbivory; detritivory; piscivory, etc.) and ontogenetic stages (juveniles and adults). The resulting species lists were then split into 20 fish groups, viz.: coastal small planktonic feeders (clupeids); coastal small demersal invertebrate feeders (catfish); coastal medium invertebrate and small fish feeders (grunts) juveniles; coastal medium invertebrate and small fish feeders (grunts) adults; coastal large demersal carnivores (groupers) juveniles; coastal large demersal carnivores (groupers) adults; small coastal detritus and plant feeders (mulletts); medium coastal fish feeders (coastal sharks); large predators (oceanic sharks); large coastal fish and invertebrate

pelagic feeders (tuna) juveniles; large coastal fish and invertebrate pelagic feeders (tuna) adults; large reef planktivores (soldierfishes); large reef carnivorous (moray); large reef herbivores (parrotfishes); small reef carnivores (blennies); small reef herbivores (damselfish); small pelagic predators (bluefish); mesopelagics; bathypelagics, and ‘other fishes.’

The master equation of Ecopath, for each functional group  $i$ , is,

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

where  $B_i$  and  $B_j$  are biomasses (or rather densities, here wet weight, in  $\text{t km}^{-2}$ ), the latter pertaining to  $j$ , the consumers of  $i$ ,  $P/B_i$  their production/biomass ratio, equivalent to total mortality under most circumstances [2,22],  $EE_i$  the fraction of production ( $P = B(P/B)$ ) that is consumed within, or caught from the system (usually left as the unknown to be estimated when solving the equation above),  $Y_i$  the fisheries catch (i.e.,  $Y_i = F_i B_i$ ),  $Q/B_j$  the food consumption per unit biomass of  $j$ , and  $DC_{ij}$  the contribution of  $i$  to the diet of  $j$ .

The parameter estimates ( $B_i$ ,  $P/B_i$ ,  $Q/B_j$  and  $DC_{ij}$ ) for 35 living groups in the model were obtained mainly by taking means of the estimates for the corresponding groups in the component models, weighted by the area represented (Table 2). For marine mammals and sea turtles groups input parameters were obtained from independent stock assessment estimates and from other studies for the same species reported in the Gulf of Mexico area.

The catches ( $Y_i$ ), consisting of landings + discards, were adapted from a number of sources, notably (NMFS [25]) for the Northern, and SEMARNAP [26] for the Southern GoM. Table 3 presents the landings and the discards considered here, aggregated from eight fleet/gear types (inshore trawling; inshore long lining; inshore gill netting; offshore trawling; offshore long lining; offshore gill netting; purse seining; miscellaneous gears and fisheries, incl. recreational fisheries).

Step 3, i.e., solving for the unknowns (generally the  $EE_i$  in Eq. (1)), was done by Ecopath, which solves this system through a robust matrix inversion routine [27]. Note that the right-hand side of Eq. (1) can also include a biomass accumulation term in cases where the biomass is known to have changed during the period under consideration, thus allowing for non-equilibrium situations and net migration, two cases not considered here.

Once an initial set of parameters were available, the model was balanced, mainly by adjusting the  $DC_{ij}$ , usually the input that is most uncertain [6]. Herein, the goal was to achieve thermodynamic equilibrium for each functional group, i.e., ecotrophic efficiencies ( $EE_i$ ) ranging between 0 and 1, and growth efficiency ( $g = \text{production/consumption}$ ) constrained between 0.1 and 0.3 (except for very small, fast growing organisms, for which value of up to 0.5 was allowed).

Validation of the model here mainly consisted of examining the stability of its behaviour in time and space, using Ecosim and Ecospace, respectively. These test runs led to minor parameter adjustments for a few functional groups.

Ecosim uses the master equation:

$$dB_i/dt = g_i \sum Q_{ij} - \sum Q_{ji} + I_i - (M_{0i} + F_i + E_i) B_i \quad (2)$$

Table 3  
Summary of landings and discards data of eight different fleets/gears used in the synthetic model of the GoM ecosystem

Functional groups	Total landings <sup>a</sup> (t 10 <sup>3</sup> year <sup>-1</sup> )	Total discards <sup>b</sup> (t 10 <sup>3</sup> year <sup>-1</sup> )	Inshore (<20 m)		Offshore (20–200 m)	
			Landings (t km <sup>-2</sup> year <sup>-1</sup> )	Discards (t km <sup>-2</sup> year <sup>-1</sup> )	Landings (t km <sup>-2</sup> year <sup>-1</sup> )	Discards (t km <sup>-2</sup> year <sup>-1</sup> )
Macroepifauna	92.9	123	0.057	—	—	0.076
Juvenile shrimps	57.6	—	0.036	—	—	—
Adult shrimps	86.5	—	—	—	0.053	—
Other decapods	50.6	215	0.019	0.01	0.012	0.123
Octopus	15.3	—	0.009	—	—	—
Clupeids	744.1	—	0.183	—	0.275	—
Catfishes	39.6	850	0.015	0.21	0.010	0.317
Juvenile grunts	—	32	—	0.01	—	0.012
Adult grunts	2.3	—	0.001	—	0.001	—
Groupers	30.3	—	0.011	—	0.007	—
Mulletts	19.5	—	0.012	—	—	—
Coastal sharks	7.9	—	0.003	—	0.002	—
Oceanic sharks	8.2	—	0.005	—	—	—
Juvenile tunas	—	23	—	—	—	0.014
Adult tunas	21.9	—	0.008	—	0.005	—
Bluefishes	4.4	—	0.001	—	0.001	—
Dolphins	—	4	—	—	—	0.003
Other groups <sup>c</sup>	8.9	127	0.003	0.03	0.003	0.044
Total	1190	1375	0.360	0.26	0.380	0.592

<sup>a</sup>Sources of landings data: NMFS and SEMARNAP data records [26,34].

<sup>b</sup>Sources of discards data: [49–54].

<sup>c</sup>The 'Other groups' consists of minor fish taxa (Batrachoididae, Cyprinodontidae, etc.), but also includes sea turtles.



where  $dB/dt$  is the rate of biomass change,  $g$  the growth efficiency (i.e.,  $P/Q$ ),  $F$  the fishing mortality (see Eq. (1)),  $M_0$  the baseline natural mortality (i.e., excluding predation),  $I$  the immigration rate,  $E$  the emigration rate, and  $Q_{ij}$  ( $Q_{ji}$ ) the consumption of type  $j$  ( $i$ ) biomass by type  $i$  ( $j$ ) organisms. Eq. (2), in Ecosim, is parameterized using the estimates in Eq. (1) for a balanced Ecopath model [16,23].

Ecospace is parameterized in a similar fashion, but runs an Ecosim model in each of its spatial cells, while allowing movements of functional groups between cells [17,23]

Step 4 consisted of running various exploitation scenarios using Ecosim, presented below along with their key results.

**5. Results and discussion**

Fig. 3 presents the 40 functional groups of the synthetic model of the GoM. The links indicating the trophic interactions between these groups, which jointly lead to a connectance index [28] of 0.23 for this food web, are omitted here for clarity’s sake. We briefly present here some quantitative features of the food web thus generated.

The total system throughput [29] is  $11,167 \text{ t km}^{-2} \text{ year}^{-1}$ . Of this,  $1,786 \text{ t km}^{-2} \text{ year}^{-1}$  consists of respiratory flows, and  $2,455 \text{ t km}^{-2} \text{ year}^{-1}$  of flows to the detritus. The relative importance of the latter flows is evaluated by Finn’s cycling index, i.e., the percentage of flows due to recycling of detritus [30]. With 14.8%, this value is near the midrange for marine ecosystems, suggesting a medium-to-high degree of maturity [31].

The mean path length in the GoM model, i.e., the average number of groups that a flow passes through, calculated as the total throughput divided by the sum of the

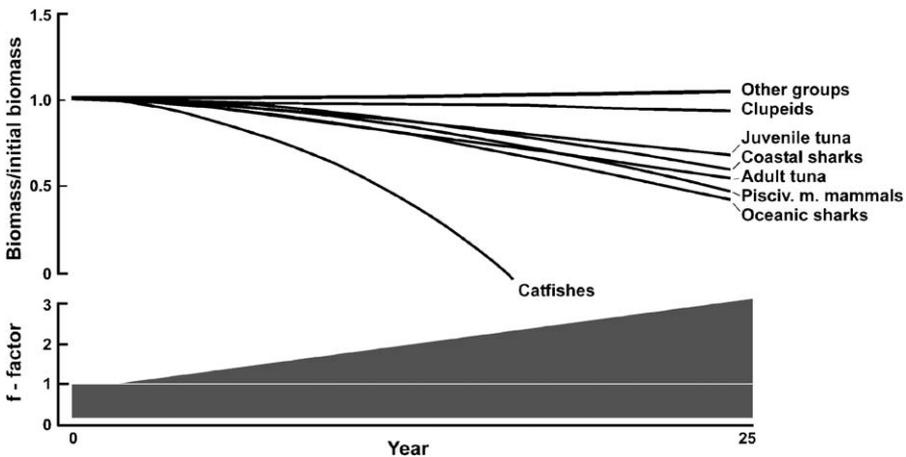


Fig. 4. Basic Ecosim scenario, used to test the dynamic behaviour of synthetic GoM model. The bottom panel shows the simulation of linear increase in effort by all fishing fleets until overall effort is tripled at year 25. The upper panel shows the response of ecosystem functional groups (Scenario #1 in Table 4). See text for details.

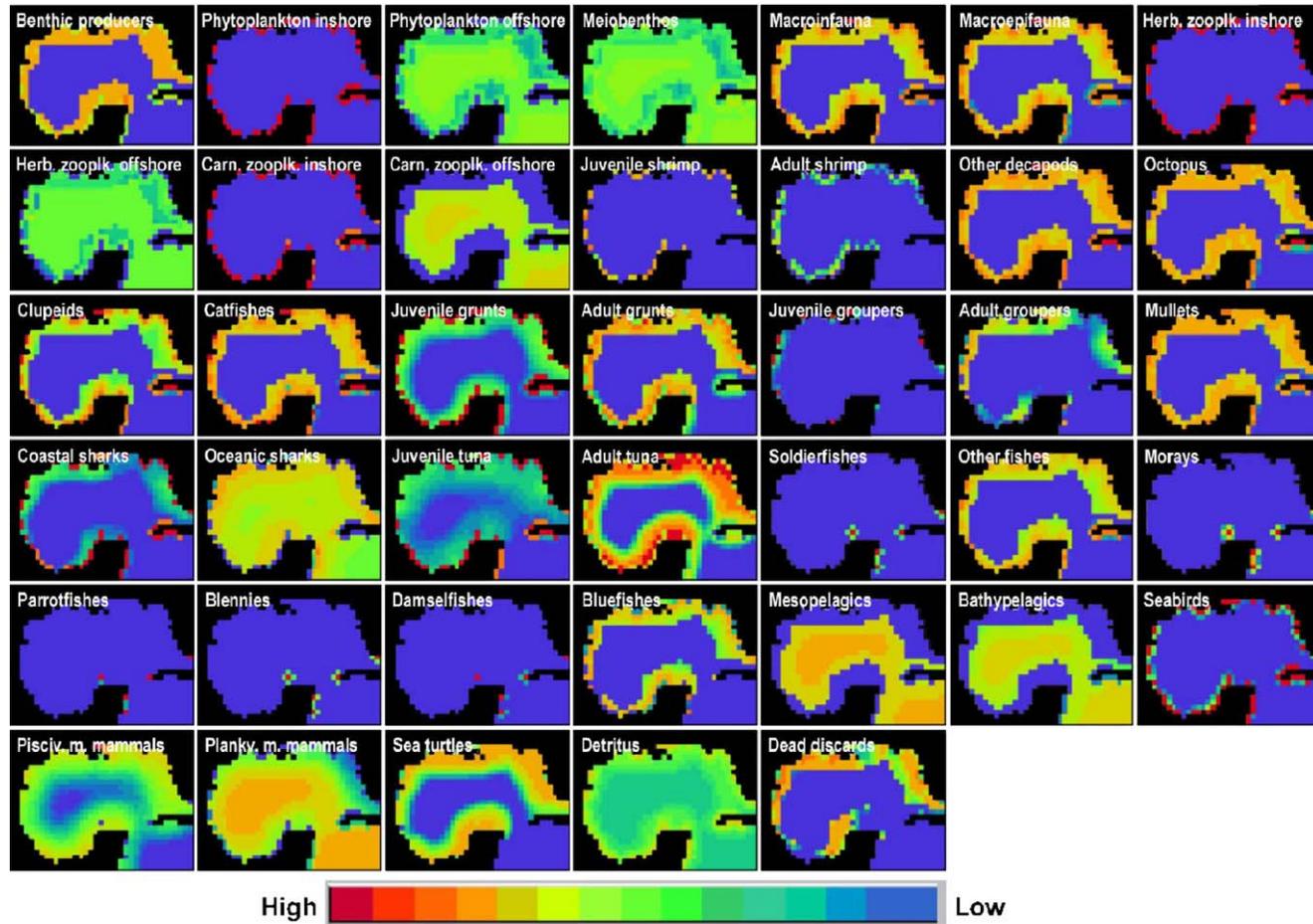


Fig. 5. Ecospace representation of the synthetic model of the GoMLME. Each panel represents the relative biomass of an ecosystem functional group with blue indicating low densities and red high. The relative densities of the functional groups are defined by their affinities to the subsystem defined in Table 1. As each of the functional groups can move between cells, the relative densities predicted by Ecospace will depend on the food and predation encountered by each group within each cell [17]. Hence, for Ecospace to predict biologically acceptable distribution implies that the underlying food web and its division into subsystems is biologically realistic (see also text).

Table 4

Changes in the GoM ecosystem components as a result of Ecosim simulations involving varying fishing effort by the coastal and offshore fleets for the 25 year time horizon

Scenario fishery effort (%) year				Results				Comments
#	Coastal	Offshore	Mixed	Groups increasing	% change	Groups decreasing	% change	
1	↑5	↑5	↑5	Sea birds	10–30	Catfish	0–60	Negative effect of by-catch, strong indirect competition of prey between predators and fisheries, positive effect in generalist groups that consume discards
				Adult grunts Juvenile grunts Bluefish		Oceanic sharks Pisc. marine mammals Adult and juvenile tuna Coastal sharks		
2	↑3–5	↑3–5	↑3–5	Sea birds	10–30	Catfish	40–80	Negative effect of by-catch, strong indirect competition of prey between predators and fisheries, affected groups can recover and settle at new level of abundance
				Adult grunts Adult groupers		Oceanic sharks Pisc. marine mammals Coastal sharks		
3	status quo	↑3	status quo	Oceanic sharks	≈ 10	Catfish	10–30	Negative effect of by-catch, strong indirect competition of prey between predators and fisheries, generalist groups benefit by discards

4	status quo	status quo	↑6	Bluefish Sea birds No substantial increase of any group	(≪10)	Pisc. marine mammals Adult and juvenile tuna Sea birds	10–30	Overexploitation of clupeids and negative effect on clupeid predators
5	status quo	↑5	status quo	Sea birds	10–30	Bluefish Clupeids Adult and juvenile tuna Pisc. marine mammals	20–30	Negative effect of by-catch, strong indirect competition of prey between predators and fisheries, generalist groups benefit by discards
6	↓3	↑3	status quo	Bluefish Oceanic sharks Adult tuna No substantial increase of any group	(≪10)	Catfish Pisc. marine mammals	≈20	Support to the idea that inshore and offshore strata are coupled and that inshore biomass does not increase if the predation in offshore waters remains high
7	↑3	↑5	↑3	Sea birds  Adult grunts Bluefish Adult tuna	10–30	Oceanic sharks Adult tuna Catfish Catfish  Oceanic sharks Pisc. marine mammals	40–80	Negative effect of by-catch, strong indirect competition of prey between predators and fisheries, generalist groups benefit by discards

exports and the respiration [32], was 3.6. This locates the GoM near the midrange of marine ecosystems.

The calculated transfer efficiencies between trophic levels are 15.1% from trophic level I to II, 13.5% from II to III, 9.6 from III to IV and 7.5% from IV to V. Here again, we observe intermediate values, as [33] show that transfer efficiencies, in marine ecosystems, range from about 5 to 25%. These transfer efficiencies allow estimation of the primary production required to sustain the fisheries catches (landings + discards), i.e., 24.5% at the lower end of estimates for shelves in [33], but still a high value.

Fisheries catches in the GoM correspond to a flux of  $1.6 \text{ t km}^{-2} \text{ year}^{-1}$ , a relatively low value (0.07% of primary production), especially since the mean trophic level of the catch, 2.9, is also low [34]. Moreover, 56% of this catch consists of discarded by-catch, mainly (73%) from trawlers. This means that of almost 3 million tonnes caught annually in the GoM per year, over half is discarded. On the other hand, this input, consumed in roughly equal parts by birds on the surface, by sharks in the water column and by crabs on the sea bottom, contributes only a small fraction (less than 1%) to the food of 'discard eaters.'

We abstain from presenting more system characteristics, as those given here suffice to illustrate the various inferences that can be drawn from a food web such as presented here. (Details on the construction of the model, and its various features, are available online at [www.saup.fisheries.ubc.ca](http://www.saup.fisheries.ubc.ca).)

The model presented above is dynamically stable, as established by running it with Ecosim and Ecospace. Specifically, the response of its functional groups to increases in fishing mortality by various fleets through Ecosim corresponds to what may be expected of an ecosystem of this type (see Fig. 4). Moreover, all functional groups maintain their biomass close to their baseline (Ecopath) value even when they distribute themselves in those parts of the GoM to which they have been assigned the highest affinities (Fig. 5). Thus, we have some confidence in the contents of Table 4, which summarizes the outcomes of seven scenarios run with Ecosim. Notably, these results confirm the inference from the analysis of the GoM food web (above), suggesting that the system is still reasonably 'mature' [35], and rather robust to exploitation.

As shown in Table 4, all scenarios where coastal fisheries were simulated to stay in status quo or to increase resulted in strong negative effects on by-catch species and, on indirect effects in associated preys or predators species. Indirect competition of prey between predators and fisheries was evident and generalist groups that consume discards (seabirds and grunts) benefited. All these changes reverberated through the entire shelf subsystem by the food web.

Moreover, strong coupling between inshore and offshore strata is evident in the system: the biomass of inshore resources does not increase substantially, even under low fishing pressure, if fishing pressure and/or predation in offshore waters remain high. This suggests a recruitment failure due to the offshore fisheries decreasing the biomass of reproductive adults.

Recent developments in the EwE software (see [www.ecopath.org](http://www.ecopath.org)) allow more refined policy analyses than presented here. This will allow revisiting the results in

Table 4, notably to identify policies that would combine continued fishing with some rebuilding of the GoMs depleted stocks.

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