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AN ECOSIM MODEL FOR EXPLORING GULF OF MEXICO ECOSYSTEM MANAGEMENT OPTIONS: IMPLICATIONS OF INCLUDING MULTISTANZA LIFE-HISTORY MODELS FOR POLICY PREDICTIONS

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ABSTRACT

An Ecopath-Ecosim ecosystem model under development for coastal areas of the Gulf of Mexico simulates responses of 63 biomass pools to changes in fisheries and primary productivity. Ten key species are represented by detailed, multistanza population-dynamics models (31 of the biomass pools) that attempt to account explicitly for possible changes in recruitment rates due to changes in by-catch rates and trophic interactions. Over a 1950–2004 historical reference period, the model shows good simulated agreement with time-series patterns estimated from stock assessment and relative abundance index data for many of the species, and in particular it offers an explanation for apparent nonstationarity in natural mortality rates of menhaden (declining apparent M over time). It makes one highly counterintuitive policy prediction about impacts of management efforts aimed at reducing by-catch in the shrimp trawl fishery, namely that by-catch reduction may cause negative impacts on productivity of several valued species [menhaden, *Brevoortia patronus* Goode, 1878; red drum, *Sciaenops ocellatus* (Linnaeus, 1766); red snapper, *Lutjanus campechanus* (Poey, 1860)] by allowing recovery of some benthic predators such as catfishes [*Arius felis* (Linnaeus, 1766), *Bagre marinus* (Mitchill, 1815)] that have been reduced by trawling but are also potentially important predators on juveniles of the valued species. Recognition of this policy implication would have been impossible without explicit, multistanza representation of juvenile life histories and trophic interactions, because the predicted changes in predation regimes represent only very small overall biomass fluxes.

Fisheries management councils have been under considerable pressure to take account of "ecosystem" effects in setting harvest policies, because of concerns ranging from impacts of by-catch and habitat damage effects by some fishing activities to impacts of fishing on capabilities of stocks to support other valued species. When harvest controls have been based only on reference points from single-species assessments, even including by-catch mortality effects, assessments do not actually ignore ecological interactions entirely but typical single-species models make very particular assumptions about how natural mortality and recruitment rates somehow remain stable despite changes in ecological circumstances (e.g., changes in predation risk and food availability). Discomfort about these very restrictive assumptions has led to investment in development of models that account explicitly for at least some major trophic interaction effects.

As part of an evaluation of ecosystem modeling tools for comparing fisheries management options in the Gulf of Mexico, the Ecosystem Scientific Committee of the Gulf of Mexico Fisheries Management Council requested development of a demonstration Ecosim model using the widely available Ecopath with Ecosim software (http://www.ecopath.org). This software facilitates management of basic biomass and trophic interaction (food-habits) data for whole ecosystems and checks for consistency of the data through the Ecopath "mass balance" process, in which estimated total mortality rates for biomass components are checked against estimated total predation and fishing-loss rates calculated from predator abundances, diet compositions, and historical fisheries data. Once a plausible (or at least physically possible without the need for spontaneous creation of mass to satisfy input predator food demands and fishery removal rates) mass-balanced biomass and trophic flow pattern has been found, the resulting ecosystem state/flow estimate can be passed to Ecosim, a dynamic model that simulates temporal responses to policy changes such as fleet reductions, along with impacts of changes in factors such as nutrient loading and primary productivity.

The Florida Marine Research Institute (FMRI) had already contracted for development of an Ecopath/Ecosim model of the West Florida Shelf (Mackinson et al., 2001; Okey and Mahmoudi, 2002; Okey et al., 2004), and that model had in turn been modified extensively to simulate effects of changing nutrient loading and fishing effort on the fishes of Tampa Bay and other Florida Fisheries Independent Monitoring (FIM) study areas. The Tampa Bay analysis demonstrated surprisingly good ability of Ecosim to fit historical time series of abundances of a wide variety of fish species, and it encouraged us to use that model as a starting point for wider analysis of the Gulf of Mexico coastal ecosystem as a whole.

Starting with the Tampa Bay biomasses, feeding ecology (consumption rates, diet compositions), and historical fishing patterns, we extended the model to whole-Gulf scale by correcting biomasses to averages over the larger area, adding a variety of species (such as red snapper and menhaden) that are not abundant in Tampa Bay, and developing a model-testing set of data that includes historical fishing-effort patterns for major fleets, estimates of abundance over time from stock assessments, historical catches, and some historical information on changes in total mortality rates (Z). In adding additional species and fisheries, we aimed to account for at least 90% of the total coastal fish (excluding tuna) and invertebrate harvest for the Gulf and to account as well for by-catch patterns and impacts for particular fisheries (especially shrimp trawling) that have been suggested to have large impact on other fish stocks.

We view the development of a complex model like the current version of the Gulf of Mexico Ecosim model as an ongoing process. That process will be facilitated by inclusion of new data and information from a variety of researchers using the Ecopath with Ecosim data-management software, but the really critical need is for continual harsh challenges of the model in the form of comparisons of its predictions to historical and spatial data and of demands for new policy predictions from it that expose (through unrealistic predictions) weaknesses in the data and model structure. Below we review just the June 2007 version of the model and compare its predictions to historical relative abundance and stock-assessment data for a variety of species for the reference period 1950–2004. We show that for one very particular fishery policy, regulation of by-catch by the shrimp fishery, the ecosystem model does indeed make predictions very different from those obtained from single-species assessment models and that these disturbing predictions arise from the particular capability of Ecosim to represent changes in predation mortality rates of prerecruitment juvenile fishes.

Model Structure and Assumptions

The current model simulates biomass dynamics of 63 biomass "pools" (Table 1), ranging from detritus and phytoplankton at the bottom of the food web to large piscivores like red snapper, mackerels (*Scomberomorus* spp.), and coastal sharks at the top of the web (no marine mammals are included in the current model version). Overviews of how Ecosim represents dynamic change in these pools over time can be found in Walters and Martell (2004) and Christensen and Walters (2004). Dynamics are simulated on a monthly time step, in two alternative model structures as described below.

Here, we do not attempt to present all equations and parameter values used in the ecosystem model; all are stored in an Access database that is freely available for download at http://www.ecopath.org/index.php?name=Models&sub=model&modelID=128. The easiest way to examine the data, test effects of alternative parameter estimates, and reproduce the results described below is to use the Ecopath/Ecosim version 5 software, again freely available at http://www.ecopath.org.

Biomass Dynamics for Aggregated Biomass Pools.—First, some pools are represented only by total biomass per unit area and are simulated by solution of differential equations for biomass rate of change of the form

$$dB_i/dt = eQ_i(t) - Z_i(t)B_i \qquad (1)$$

where B_i is biomass of pool i, e is a food conversion efficiency, $Q_i(t)$ is total rate of food consumption by the pool, and $Z_i(t)$ is instantaneous total mortality rate for the pool as a result of unexplained causes plus predation plus fishing. $Q_i(t)$ is calculated as a sum of consumption rates of various prey types, according to preferences defined initially by Ecopath diet-composition inputs. The components of $Q_i(t)$ also form components of the total mortality rates $Z_j(t)$ of the prey types eaten by each pool. Total mortality rate at any time is represented by the sum

$$Z_i(t) = Mo_i + \textstyle\sum_j Q_{ij}(t)/B_i(t) + \sum_k q_{ki}E_k(t) \qquad (2)$$

where Mo_i is an unexplained natural mortality rate, predation rates $Q_{ij}(t)$ represent total consumption rates of pool i by pool j predators, and fishing mortality rates $q_{ki}E_k(t)$ imposed by fishing fleets k (including landed catches, by-catch, and dead discards) are represented as varying with time-dependent fishing efforts $E_k(t)$ ($k = 1 \ldots 18$ in the current Gulf of Mexico model, Table 2). Efforts are scaled so that $E_k(0) = 1$, i.e., are scaled to 1.0 at Ecopath base conditions, allowing estimation of "catchabilities" q_{ki} as $q_{ki} = C_{ki}(0)/B_i(0)$ where $C_{ki}(0)$ is an Ecopath base catch of species i entered for each fishing effort k. The q_{ki} can also be made density dependent [on $B_i(t)$ through a function of the form $q_{ki}(t) = q_{\max}/(1 + kB_i(t))$] where k is chosen so as to make q_{ki} equal to the Ecopath base value when $B_i(t) = B_i(0)$; this option is particularly important for correct prediction of historical catches of menhaden, for which catchability is obviously density dependent (Vaughan et al., 2000).

Each component consumption/predation rate $Q_{ij}(t)$ of prey type i by pool j is predicted by the "foraging arena" consumption rate equation

Table 1. Biomass pools included in Gulf of Mexico Ecosim model and Ecopath base input estimates of biomass, production per unit biomass (or total mortality rate Z for multistanza population components), total food consumption per unit biomass, ecotrophic efficiency defined as proportion of Z explained by modeled predation and total catches (landings plus by-catch and discards). Pools indicated by italicized names are represented by differential equation model, others as stanzas within single-species age-structured models. Note that low ecotrophic efficiencies for some groups imply not a lack of predation mortality but only that mortality is not explicitly explained by modeled predator groups or fisheries. Numbers before organism names represent months of age.

Group name	Biomass (mt km^{-2})	Prod./biom. (Z, yr^{-1})	Cons./biom. (yr^{-1})	Ecotrophic efficiency	Trend data sources
0–12 Snook	0.000217	5	25.5123	0.5008	
3–12 Snook	0.0185	2	6.268	0.008	
12–48 Snook	0.2272	0.9	2.3628	0.0978	
48–90 Snook	0.0984	0.62	1.4982	0.5751	
90+ Snook	0.02	0.6	1.3	0	Muller and Taylor (2006)
0–3 Red drum	0.000181	2	18.7423	0.5024	
3–8 Red drum	0.00493	3.5	6.699	0.0335	
8–18 Red drum	0.0323	1.1	2.9886	0	
18–36 Red drum	0.1284	0.6	1.7166	0.1713	
36+ Red drum	2	0.15	0.95	0.0002	Porch (2000), Murphy (2005)
0–3 Sea trout	0.000091	6	23.1667	0.7594	
3–18 Sea trout	0.026	1.4	4.0109	0.1337	
18+ Sea trout	0.22	0.7	1.6	0.3279	FIM sampling
0–3 Sand trout	1.97E-05	5	37.8657	0.225	
3–12 Sand trout	0.00252	1.2	8.7796	0.4279	
12+ Sand trout	0.1	0.7	2.7	0.2394	
0–6 Mullet	0.0343	3	50.018	0.5123	
6–18 Mullet	0.5224	1.8	18.2253	0.3774	
18+ Mullet	2.8	0.8	8	0.5428	Mahmoudi (2005)
0–3 Mackerel	3.68E-05	4	73.1333	0.0393	
3+ Mackerel	0.25	0.7	6	0.572	SEDAR 5 (2004)
0–10 Ladyfish	0.00979	2.8	17.8409	0.6864	
10+ Ladyfish	0.089	1.6	6	0.1537	
0 Grouper	0.0045	2	33.1643	0	
1–3 Grouper	0.0246	0.6	14.9354	0.1357	
3+ Grouper	0.52	0.45	6	0.4275	Stochastic SRA
Jacks	0.2891	0.8	2	0.9	
Bay anchovy	1.3653	2.53	14	0.6	FIM
Pinfish	0.75	1.019	8	0.9507	FIM
Spot	0.8	1.1	12	0.8328	FIM
Silver perch	1.7134	1.4	9	0.9	FIM
Scaled sardine	11	1.8	12.106	0.5487	SEAMAP
Mojarra	0.631	1.9	15	0.8	FIM
Threadfin herring	0.08	1.31	12.5	0.3655	FIM
0–12 Menhaden	1.5336	2.3	14.5312	0.5797	
12+ Menhaden	6	1.9	6	0.6973	Vaughan et al. (2000)
Menidia (silverside)	0.16	2.3	16	0.8815	FIM
Catfish	0.15	0.8	7.6	0.9377	FIM
Bumper	0.15	1.2	12	0.8545	FIM

Table 1. Continued.

Group name	Biomass ($mt\ km^{-2}$)	Prod./biom. (Z, yr^{-1})	Cons./biom. (yr^{-1})	Ecotrophic efficiency	Trend data sources
Caridian shrimp	4.2561	2.4	18	0.6	
Shrimp	1	2.4	19.2	0.9233	NMFS catch, effort stats.
Stone crab	0.1675	2	7	0.4	
Blue crab	0.2	2.4	8.5	0.584	FIM
Cyprinodontids	0.9	2.5	10	0.0897	FIM
Poecilids	0.05	2.5	10	0.4511	
Pigfish	0.2072	0.8	4	0.75	FIM
Gobies	0.179	1.5	7.5	0.75	FIM
Rays	4	0.3	1	0.2502	
Pompano	0.1	1	8	0.7	
Lobster	0.025	0.8	5	0.5	SEDAR 8
0–6 Red snapper	0.00889	3	61.3643	0	
6–24 Red snapper	0.1929	2	19.4157	0.2591	
Older red snapper	0.55	0.6	8	0.1461	Stochastic SRA, SEDAR 7 (2005)
Atlantic croaker	0.6	1.5	10	0.8576	Ortiz et al. (2000)
Large coastal sharks	12	0.08	1	0.075	SEDAR 11 (2006)
Benthic invertebrates	31.7911	4.5	22	0.8	
Macrozooplankton	10.734	22	67	0.5	
Microzooplankton	7.6421	36	89	0.5	
Infauna	20	2	10	0.1	
Attached microalgae	29.778	25	—	0.1821	
Sea grass	175.617	9.014	—	0.0024	
Phytoplankton	25	182.13	—	0.3237	
Detritus	100	—	—	0.1091	

$$Q_{ij}(t) = v_{ij}a_{ij}T_i(t)B_i(t)B_j(t)/(2v_{ij} + a_{ij}T_j(t)B_j(t)) \tag{3}$$

This rate equation can optionally also be modified to represent prey-switching (change in a_{ij}) effects, prey-handling time, and reduction in foraging time in direct response to increases in predation risk; we have not used any of those advanced options in the Gulf of Mexico model to date. In the basic foraging arena consumption equation, the rate constant v_{ij} represents "flow" of prey from behaviorally (or locationally) invulnerable to vulnerable states (which can limit predation rates to levels far lower than would be predicted from simpler mass-action models and create strong "apparent competition" among predators through the denominator term of the equation), a_{ij} represents rate of effective search or search efficiency for predator i on prey type j, and $T_i(t)$ represents the relative amount of time that individuals of type i (and j) spend foraging and hence at risk of predation. Temporal adjustments in $T_i(t)$ occur in the simulations when per-capita feeding rates (Q/B) drop below Ecopath input values; such adjustments lead to (1) density dependence in predation risk, because animals spend less time at risk of predation when competitors are fewer, and (2) type II functional response forms (animals try to keep total food intake constant, by changing T_i, when any or all prey types become less or more abundant). The a_{ij} parameters can be calculated from Ecopath diet input data, whereas the v_{ij} parameters must be estimated for each pool by statistical fitting of the dynamics to

Table 2. Fisheries included in initial Gulf of Mexico Ecosim model and main biomass pools affected by each. Average fishing mortality rate estimates for 2000–2004 represent Ecopath base input fishing rates times estimated relative fishing effort for the recent period. Note that species-specific fisheries (last several table rows) include F components due to both recreational and commercial line fishing; fisheries with those general names are used only to affect species for which species-specific fishing-rate histories have not yet been assessed or entered into the Ecosim framework.

Fishery	Main species affected and estimated fishing rates (F) for 2000–2004
Gill/cast net	6–18 mullet (0.21), 18+ mullet (0.167), pompano (0.09)
Purse seine	bay anchovy (0.05), menhaden (0.63), sharks (0.002)
Haul seine	none with F > 0.01
Recreational hook and line	12–48 snook (0.08) ladyfish (10+ (0.10), catfish (0.06), pompano (0.43)
Crab traps	stone crab (0.21), blue crab (0.58)
Cast nets	mullet effect included in gill/cast net above; no others with F > 0.001
Bait trawl	none with F > 0.01
Commercial hook and line	all included in species-specific fisheries below
Shrimp trawl	1–3 grouper (0.08) jacks (0.69) pinfish (0.01), spot (0.5) silver perch (0.88), scaled sardine (0.05), threadfin herring (0.13), menidia (0.31), catfish (0.67), shrimp (0.8), pigfish (0.14), gobies (0.56), rays (0.08), 6–24 red snapper (0.52), Atlantic croaker (0.5)
Lobster pot	lobster (0.4)
Shark fishing	sharks (0.02)
Snook fishery	48–90 snook (0.18)
Red drum fishery	18–36 red drum (0.37)
Trout fishery	18+ sea trout (0.29), 12+ sand trout (0.21)
Grouper fishery	3+ grouper (0.33)
Snapper fishery	24+ snapper (0.24)
Mackerel fishery	3+ mackerel (0.14)

time-series data (low v_{ij} values imply "bottom-up control" of production and mortality, and strong compensatory responses of each population to reductions in its own abundance; in time-series settings, we look for two types of effects indicating low vulnerability—lack of response of prey mortality rates to changes in predator abundance and strong predator compensatory responses, analogous to steep stock-recruitment curves).

Biomass pools represented by means of the differential-equation approach (arranged in no particular order of trophic position or importance to system function) are indicated by italicized pool names in Table 1. Note that this list includes some important harvested species (shrimp, crabs, sharks, pompano) along with a variety of "forage base" species and primary producers.

Age-structured Dynamics for Species with Complex Trophic Ontogeny and Size-age–Dependent Fishery Impacts.—The second basic simulation approach in Ecosim is to simulate monthly changes in numbers and relative body weights of monthly age cohorts of species that undergo complex trophic and fisheries-impact ontogeny. Ecosim allows any species to be split into an arbitrary number of age (in months) "stanzas" and prey preferences and vulnerability to various predators (and fisheries) to be treated as constant over the months of age included within each stanza. Stanza age breaks can represent both ontogenetic shifts in habitat and diet and changes in vulnerability to by-catch and retention fisheries. We used as many as five stanzas [Table 1, red drum and snook, *Centropomus undecimalis* (Bloch, 1792)] to represent species with very complex ontogeny and fisheries selection patterns and as few as two stanzas for others, e.g., menhaden. In one case (red snapper), stanza breaks were chosen specifically to represent a particular age range (6–24 mo) for which vulnerability to by-catch impact is known to be highest.

Monthly (age a) changes in numbers [$N_{ia}(t)$] and relative weights [$w_{ia}(t)$] within each pool i representing a life-history stanza within a species "s" are predicted from the survival-growth equations

$$\begin{aligned} N_{ia+1}(t+1) &= N_{ia}(t)\exp(-Z_{ia}(t)) \\ w_{ia+1}(t+1) &= w_{ia}(t) + e_{ic}qn_{ia}(t) - m_s w_{ia}(t) \end{aligned} \tag{4}$$

Here, $Z_{ia}(t)$ is the total mortality rate (sum of unexplained, predation, and fishing components as for non-age-structured pools), e_{ia} is a size- and species-specific growth efficiency, $q_{ia}(t)$ is relative food consumption rate of age a individuals predicted from the foraging-arena equation at an assumed predation rate proportional to $w_{ia}(t)^{2/3}$, and m_s is a metabolic rate for species s again chosen so as to make growth match a von Bertalanffy curve with metabolic coefficient K_s. The per-capita predation rate $qn_{ia}(t)$ is calculated from predicted total consumption $Q_i(t)$ as $qn_{ia}(t) = Q_i(t) w_{ia}(t)/\Sigma_a N_{ia}(t)w_{ia}(t)$; in the foraging-arena equation calculation of $Q_i(t)$, $B_i(t)$ is replaced by the relative total search area or volume $P_i(t) = \Sigma_a N_{ia}(t)w_{ia}(t)^{2/3}$. Growth efficiencies and search-rate parameters for the foraging-arena equation are calculated from vulnerability estimates and from initial consumption rates $Q_i(0)$ entered in Ecopath for one leading stanza i.

Because a biomass-age pattern (and food consumption–age pattern proportional to $w^{2/3}$) like that in Figure 1 must be satisfied once stanza-specific base Z's have been specified for every stanza, Ecopath/Ecosim users are only allowed to enter initial biomass $B_i(0)$ and food consumption per biomass, $Q_i(0)/B_i(0)$, for one stanza (biomass pool i) for each multistanza species s. Then B and Q/B are calculated for the other stanzas from the relative (per recruit) biomass and food consumption rates summed over ages in those stanzas.

Initial numbers entering the first stanza for multistanza species s each month are assumed to be proportional to total egg production, and egg production is assumed to be proportional to body weight minus a weight at maturity $w_{s,mat}$. That is, $N_{i,1}(t) = k_s\Sigma_a N_{ia}(t)(w_{ia}(t) - w_{s,mat})$. The effective fecundity parameter, k_s is calculated from initial numbers, $N_{i,1}(0)$, and these initial numbers are calculated in turn from Ecopath input values of biomass for one "leading" stanza for each species s, along with initial survivorships to age calculated from initial Ecopath input values of $Z_{ia}(0)$. For these calculations, relative body weights, $w_{ia}(0)$, are set initially to the von Bertalanffy prediction, and weight is assumed to vary as the cube of length, as $w_{ia}(0) = (1 - e^{-Ksa})^3$.

For typical species like red drum, a striking pattern appears when biomasses are calculated by stanza [$N_{ia}(0)w_{ia}(0)$ are summed over ages a within each stanza] with Ecopath initial survivorship and growth estimates (Fig. 1). Such calculations generally predict much, much lower biomasses of younger stanzas than of older fish. Because predation components of $Z_i(t)$ are calculated from predicted predation rates relative to biomass available, i.e., as M components $M_{ij}(t) = Q_{ij}(t)/B_i(t)$ for each predator j, very small total predator consumptions $Q_{ij}(t)$ cause very high M components for juvenile stanzas having low $B_i(t)$. Because the prediction of $Q_{ij}(t)$ is parameterized from Ecopath predator abundance, consumption per biomass, and diet composition [so $Q_{ij}(0)$ is set to $Q_j(0)DC_{ij}$ where DC_{ij} is the Ecopath input proportion of predator j

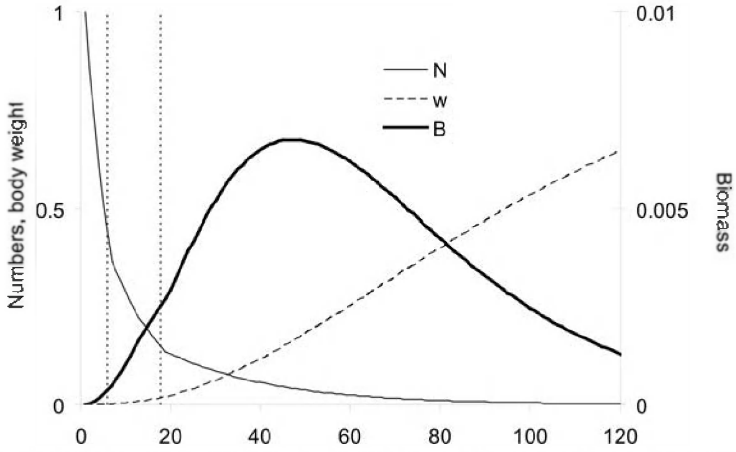

Figure 1. Typical changes in numbers, body weight, and biomass with age for a multistanza population in Ecosim. In this example, von Bertalanffy K = 0.2 yr^{-1}, and the three stanzas marked by dotted lines have the following total mortality rates, Z: 2.0 yr^{-1} for age 1–6 mo, 1.0 yr^{-1} for age 7–18 mo, and 0.5 yr^{-1} for ages 19+ mo. Note that total biomass, measured by area under biomass curve (B), is very low for the 1- to 6-mo early juvenile stanza compared to those for older stanzas.

food consumption that is prey *i*], only a tiny diet fraction DC_{ij} is generally necessary for any abundant predator *j* to cause a high predicted *M* for stanza *i* individuals. Put another way, the modeled importance of predators to juvenile survival rates is critically sensitive to diet composition assumptions involving very small diet proportions that are difficult or impossible to estimate from the field diet data that are typically available. Development of methods for estimating predation impact (partitioning juvenile mortality rates) by means other than predator diet composition data is critically needed; one possibility is based on tagging methods that permit identification of mortality agent when tagged fish die or are eaten.

When incorporated into an Ecosim model, this population-dynamics framework can produce compensatory responses through three mechanisms. First, increases in abundance of a species can result in ecosystem-scale reductions in its prey abundances and increases in its predator abundances, leading to reduced growth rates and higher mortality rates at various stanzas. Such ecosystem-scale effects are relatively uncommon in models that we have developed. Second, changes in abundance of a species can lead directly to reduced feeding and body-growth rates resulting from increased competition in restricted foraging areas/times whether or not ecosystem-scale prey abundances are affected, resulting in reduced fecundity at high abundances. This mechanism typically involves long time lags and tends to predict population cycles. Third and most important, foraging-time [$T_i(t)$ in the foraging-arena equation] adjustments to increasing $N_i(t)$ for juvenile stanzas tend to cause increased predation mortality rates as juvenile numbers increase. These rate changes lead to predicted overall recruitment relationships of Beverton-Holt form (Walters and Korman, 1999), but note that we do not explicitly build such forms into the model, as is common practice in single-species models and some multispecies models (e.g., MSFOR, Sparholt, 1995).

FISHERIES DEFINITIONS AND ESTIMATED IMPACTS.—Model development to date has concentrated on ecological data and interactions, and the complex fishery structure of the Gulf of Mexico has not been represented in great detail (Table 2). At present the model definitions include three basic types of fisheries.

First, four major fisheries are cleanly defined by gear type and target species (shrimp trawl, menhaden purse seine, lobster pot, crab pot), and usable historical effort data are available for use in setting relative efforts for model runs that attempt to represent historical fishing impacts. Only one of these, shrimp trawl, has major by-catch impacts on a wide variety of species as summarized in Table 2 (these by-catch rates were estimated from U.N. Food and Agriculture Organization reviews [Alverson et al., 1994) and from by-catch estimates used in various assessments (Ortiz et al., 2000)].

Second, a "grab bag" of fisheries, mainly represented as having minor current impact, can be defined by broad gear types such recreational line fishing and haul seining. No long time series of data are available on efforts for these gear types, so they are represented as constant over time in model-fitting tests. They do include a few high-impact fisheries, such as recreational line fishing for pompano, for which time series of species-specific fisheries impacts are not yet available for stock-assessment modeling.

Third, a set of species-specific fisheries exists for which stock-assessment methods like stock-reduction analysis (see, e.g., Kimura et al., 1984; Walters et al., 2006) have allowed estimation of total historical fishing mortality rates, summed over all gear types, and for which fisheries management involves setting species-specific fishing mortality rate and catch regulations. For these fisheries, we have not attempted to model the allocation of harvest among gear types and have chosen instead to estimate relative fishing effort over time as $E_k(t) = F_i(t)/F_i(0)$, where the $F_i(t)$ estimates are from stock assessment models for pool i representing dominant catch for the target species of the fishery and $F_i(0)$ is the Ecopath base or reference fishing rate.

In using aggregate fishing mortality rates for several important fish species, we are failing to represent one of the most serious policy issues facing fisheries management in the Gulf of Mexico. For the last six fisheries listed in Table 2, recreational fishing demand is growing, and recreational fishing mortality is increasing relative to commercial fishing mortality. Because recreational fishing effort is difficult to manage, regulatory efforts have favored use of minimum and slot size limits to limit recreational fishing mortality, but such limits result in high and growing discard rates and associated discard mortality. In at least one case (groupers), recent SouthEast Data, Assessment, and Review (SEDAR) assessments indicate that the recreational discard mortality now exceeds combined landings from all gears (SEDAR 12, 2006); we include such estimated discard mortalities in the $F_k(t)$ estimates derived from stock-assessment data but have not attempted to predict how they might grow in the future.

FITTING AND COMPARISON OF THE MODEL TO HISTORICAL TIME-SERIES DATA

HISTORICAL DATA SOURCES.—We obtained basic abundance estimates (Ecopath inputs, Table 1) wherever possible from SEDAR (http://www.sefsc.noaa.gov/sedar/)

reports and stock-assessment reports from Florida's Fish and Wildlife Research Institute (FWRI, http://research.myfwc.com/features/default.asp?id=1035) or by scaling survey catch rates from the FIM and southeast SEAMAP databases using catchability estimates provided by FWRI researchers. For some species (e.g., menhaden) we back calculated initial 1950 abundances by assuming catch $C = FB$ so $B = C/F$, then used National Marine Fisheries Service (NMFS) catch statistics for the Gulf of Mexico to provide C and more recent stock assessment results to provide estimates of likely F as of 1950.

We obtained estimates of baseline total mortality rates (P/B or Z) wherever possible by examining age- and size-composition data (from, e.g., Vaughan et al., 2000, for menhaden) or predicted them for unfished species from rough assessments of body growth (von Bertalanffy K) and the Pauly (1979) relationship between growth and M. Ecopath mass-balance calculations help considerably to bound these Z parameters, by comparing calculated baseline total removal rates (Z_iB_i) for each pool i to calculated total removal rates due to catches (and discards) and calculated predation mortality rates (Eq. 2). Ecotrophic efficiencies (Table 1) summarize the proportion of assumed Z for each pool accounted for by predation and catches, and for most pools (with notable exceptions like shrimp) we were able to account for only a relatively small proportion of the likely total Z.

Estimates of baseline food consumption rates (Table 1 Q/B estimates) were mainly obtained from bioenergetics information summarized in FishBase (http://www.fishbase.org) and were typically assumed to be 5–10 times the "production" rates Z. Significantly, more complex Q/B estimates based on bioenergetics models were not available for any of the species modeled. Again the Ecopath mass-balance procedure helped to bound Q/B estimates, because severe overestimates lead (along with diet-composition estimates) to food intake demands higher than could be satisfied by assumed production rates of prey species.

The most difficult Ecopath baseline information to obtain was diet composition, especially for younger stanzas of key species. Further, as noted above and in Figure 1, for small juvenile fish only a tiny (e.g., 0.00001) diet proportion DC_{ij} is necessary for abundant predators j to cause very high mortality rates for juveniles. In general we had to guess at diet compositions on the basis of "expert opinions" of FWRI scientists, unpublished diet reports that often gave only crude compositions (like "fish," "shrimp," "other invertebrates"), and reasonable assumptions based on relative prey and predator sizes along with general life-history information on likely habitat overlap and encounter patterns. If SEDAR-like processes are to be applied to ecosystem models for the Gulf of Mexico and other regions, regional databases of diet-composition data must be developed (J. Simons, North Carolina Department of the Environment and Natural Resources, pers. comm.).

Historical-abundance trend and fishing effort/mortality rate data for model fitting and testing were again extracted wherever possible from SEDAR and FWRI stock-assessment reports and from FIM and SEAMAP summaries of mean survey catch rates. Historical catch statistics were extracted from the National Marine Fisheries Service catch database (http://www.st.nmfs.gov/st1/commercial/index.html and http://www.st.nmfs.gov/st1/recreational/index.html). In some cases [groupers; red snapper; lobster, *Panulirus argus* (Latreille, 1804); mullet, *Mugil cephalus* Linnaeus, 1758; and red drum] for which SEDAR and FWRI assessments only covered recent years, we also ran stochastic stock reduction analyses (SRA) using the software described by Walters et al. (2006) to back calculate stock size and fishing-mortality rate trends for 1950–2004. The SRA and SEDAR stock trends have generally given similar results. Although the absolute abundance trends from single-species assessments and SRA were deliberately developed to cover the whole Gulf of Mexico, any of the relative-abundance trend data from sources like FIM and SEAMAP may not be representative of average coastal trends for the Gulf of Mexico as a whole.

FITTING PROCEDURES.—We used a four-step procedure to "calibrate" the model to historical time-trend data. The first step was an overall screening for possibly incorrect input parameters, and the next steps involved formal model-fitting procedures and sensitivity tests for effects of changes in model structure. First, we examined each species for which long-term trend data were available, to ensure that the model (1) gave reasonable fits to historical catch trends, i.e., gave reasonable temporal patterns of the product $F_i(t)B_i(t)$, and (2) gave temporal trends in $B_i(t)$ similar to those estimated from stock assessments based on catch and relative-abundance trend data. This first step led to various adjustments in both the Ecopath base inputs, particularly $B_i(0)$ and $Z_i(0)$, and some of the vulnerability parameters v_{ij}. When vulnerabilities v_{ki} of prey k to a predator i are set too low in Ecosim, the model typically predicts "flatline" dynamics involving very strong compensatory responses to increases in mortality rates due to fishing and therefore often too little decline in responses to historical increases in fishing mortality. We manually adjusted the v_{ki} for some stanzas of some species i to eliminate several obvious examples where the Ecosim v_{ki} default values [equal to $2M_{ki}(0)$] were set too low.

Second, we used a maximum-likelihood procedure to search for better-fitting estimates of a limited number (up to 50) of vulnerability exchange rates v_{ij} to which the model likelihood was found to be most sensitive. The likelihood function for fitting was taken to be (see Walters and Martell, 2004, and Walters and Ludwig, 1994, for details)

$$\ln(L) = \quad \sum_d (n_d/2)\ln\left[\sum_t (y_{dt} \quad \hat{y}_t)^2\right] \tag{5}$$

where the index d refers to time-series data set (a time series of catches, relative abundances, direct estimates of total mortality rate Z from age-size composition, relative stock sizes from stock assessment model outputs), n_d is the number of independent observations in the dth data set, y_{dt} is the observation of type d for year t, and $\hat{y}_t$ is the Ecosim prediction of that observation. Ecosim predictions are of two types, absolute and relative. For absolute observations (catch, total mortality rate, total biomass per area), $\hat{y}_t$ is just the Ecosim prediction of the quantity. For relative observations (all abundance time series used in this analysis), $\hat{y}_t = q_d B_{it}$, where B_{it} is the Ecosim predicted biomass and q_d is the conditional maximum likelihood estimate of the catchability (units scaling) parameter for the relative series. q_d is given simply by the arithmetic average of the $\ln(y_{dt}/B_{it})$ values for the series). Note that the likelihood function represented by Eq. 5 is "self weighting" over the data series, because it is derived by integration over possible values of the variance of each series d; this convention can be overridden in Ecosim if we wish to place more or less weight on any data series deliberately, but we did not find that capability necessary to deal with contradictory or uninformative data sets.

Third, we estimated a time series of annual (1950–2004) apparent nutrient-loading or primary-production "anomalies" for the Gulf of Mexico ecosystem as a whole (analogous to estimating process errors in single-species stock assessment). For each year, modeled primary production rates (phytoplankton, microalgae, sea grass) were multiplied by an arbitrary time multiplier p_t, where $p_t = 1$ by default. The same nonlinear search procedure used to vary v_{ij} values so as to maximize the likelihood of the time-series data (Eq. 5) was then allowed to vary the p_t values as primary production "anomalies" on the assumption of a prior variance of 0.1 for each p_t. In earlier fitting tests for the Tampa Bay version of the model, we had found that, over time, fitted p_t values behaved similarly to p_t values calculated from annual nutrient loading estimates for the bay. For the Gulf as a whole, we found that shared or ecosystem-scale p_t values do not explain much of the time series variation over multiple species and data types, though some model-fitting trials did suggest a slow decline in overall productivity (about 20%) since 1950, possibly due to loss of coastal estuarine habitats around the mouth of the Mississippi River. Other fitting trials, however, in which productivity was described by a smooth spline function (rather than annual values) and fewer vulnerability parameters were estimated, resulted in a dome-shaped productivity signal with a peak in the mid-1980s as might be expected from historical patterns of nutrient loading to the Gulf from the Mississippi (Scavia et al., 2003).

Fourth, we tested effects of major changes in model structure by constructing a much simplified model with 20 fewer biomass groups, by omitting a few species like snook that do not occur Gulf-wide and by aggregating various species of small fish into overall "forage fish" groups. This model gave results and fits to data essentially identical to the more complex model and will probably be used in future model development and policy exploration.

Finally, to evaluate how sensitive the procedure for fitting vulnerabilities and forcing-function parameters is for evaluating the impact of shrimp trawling, we evaluated combinations of fitting procedures in which we fitted vulnerabilities for 0–59 consumer trophic linkages (i.e., from none to all nonzero diet linkages, estimating one vulnerability parameter per linkage) and in which we fitted primary production anomalies using a spline function with from 0 to 40 splines as well as with (54) annual data points. Each such fitting trial was started at default parameter values provided by the Ecopath software. The consumers to include in each of the fitting rounds were selected on the basis of a sensitivity test, in which groups were included in order of impact on the residuals.

ABILITY OF THE MODEL TO EXPLAIN HISTORICAL ABUNDANCE TRENDS.—Despite obvious deficiencies in key input data such as diet compositions, the model is surprisingly good at reproducing basic trends in relative abundance for most Gulf biomass pools (Fig. 2). Note that simulated biomass, Z, and catch trajectories (solid lines in Fig. 2) are calculated forward over time, starting with 1950 Ecopath base values, and vary over time only in response to input time series of fishing efforts and relative primary productivities (p_t). That is, the model is not readjusted or reset at each time step so as to agree with the data, so if some functional relationship or rate were badly wrong, the equations could easily predict gross divergence of the predictions from observed trends. In other words, Figure 2 shows quite a harsh test of the ability of the model to "stay on course" over long periods of time relative to the data, given only "known" forcing changes associated with fisheries development and regulation (along with modest effects of productivity changes). For a few species like catfishes, we initialized the model with lower biomasses representative of recent years (2000); in those cases, the model predicts rapid biomass increase toward the higher levels

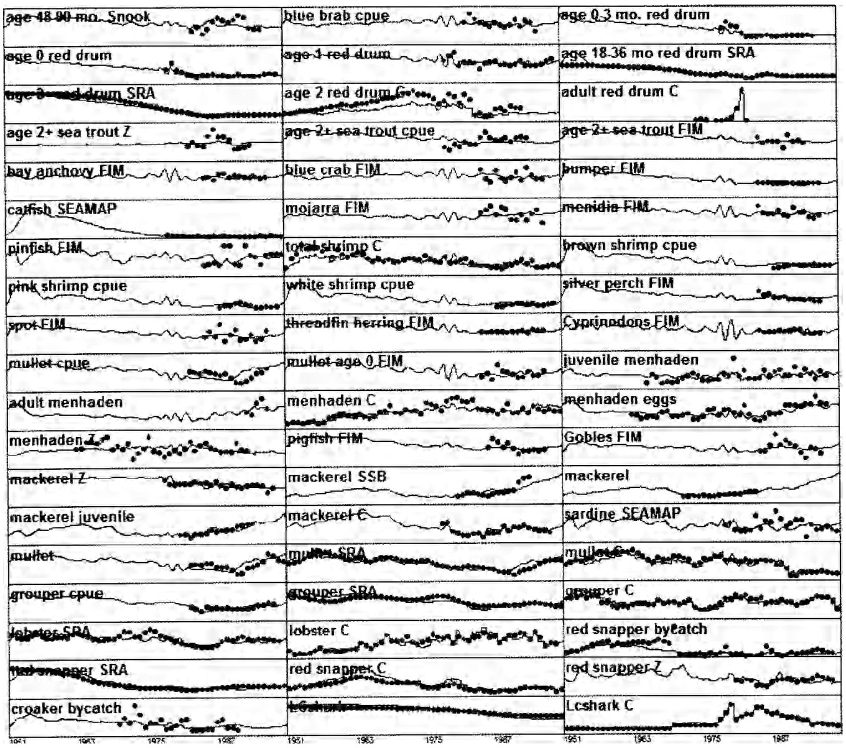

Figure 2. Predicted (solid lines) changes in a variety of biomass (B), harvest (C), and total mortality rate (*Z*) indices for the Gulf of Mexico Ecosim model, compared to time-series data (dots). All abundance time series were treated as relative abundances (scaled to same average as model predictions). Numbers before names represent months of age. CPE, catch per effort; N, numbers; red, red drum; PS, purse seine; SRA, stock reduction analysis; Alt, alternate; FIM, Florida fishery independent monitoring; CPT, catch per FIM tow; NMFS, National Marine Fisheries Service; shr (brn, pnk, whi), shrimp catch per efforts by species brown, pink, white; red sn, red snapper juvenile; LCshark, large coastal sharks; *X*-axis for each graph is time, 1950–2004.

that were probably present when fishing mortality rates were lower in the 1950s (e.g., shrimp trawl by-catch of catfish). Resetting such species to have higher initial biomasses did not substantially change the model predictions about recent biomass levels or interaction patterns.

Most of the strong changes in Figure 2 are associated with direct impacts of fishing. Several long-lived fishes have declined considerably because of historical “overfishing” (red drum, red snapper, groupers, mullet, lobsters). Two species (mullet, mackerels) have exhibited spectacular recoveries associated with severe fishery reductions (e.g., the Florida constitutional amendment in 1995 banning gillnet fishing for mullet). Perhaps the most interesting series from an ecosystem perspective are for menhaden. The age composition data in Vaughan et al. (2000) indicate that *Z* for Gulf menhaden has been decreasing over time, despite increases in fishing effort. The Ecosim model explains this pattern as being due to decreases in the menhaden *M* over time, in turn due to reductions of some key predator populations, particularly sharks (mainly due to directed shark fishing, not to by-catch of sharks in the menhaden fishery; see SEDAR 11, 2006) catfishes, and red drum (Fig. 3). The reduction in catfish predation is predicted by Ecosim to have been due to increases in by-catch/discard mortality in the shrimp trawl fishery.

A few species, particularly pinfish [*Lagodon rhomboides* (Linnaeus, 1766)] have shown large, abrupt declines followed by rapid recoveries that are not explained by the Ecosim model's trophic and fishery interactions. Interestingly, we can explain the abrupt declines by including in the model a pseudofishery named "red tide," such that high effort for this fishery causes high pinfish mortalities and "effort" is estimated over time from historical plots of relative cell counts of toxic algae along the southwest coast of Florida (Walsh and Steidinger, 2001; FWRI, 2002). Interestingly, other model predictions change very little (as indicated by measures of goodness of fit to historical data) when the red tide pseudofishery is turned on or off.

Preliminary Analysis of Critical Policy Issues for Multispecies Management

Our ability to fit historical data as in Figures 2 and 3 does not prove that the Ecosim model will give correct predictions about impacts of substantial changes in Gulf of Mexico fishery management. Beyond a few obvious trends due to high exploitation rates, good model fits could be occurring for the wrong reasons, particularly in relation to issues of trophic support and by-catch impacts. A much more important challenge for the model is to determine whether it gives credible predictions of response to major policy changes, particularly in relation to policies that have major implications for trophic support (food supply) and predation regimes. Below, we describe model predictions for a few diagnostic policy tests related to widely debated issues in the Gulf of Mexico.

Rebuilding Stocks That Have Historically Been Overfished.—Several fisheries for long-lived species that have historically been overfished have been, or are likely to be, severely restricted. All of these species feed (at least as juveniles) on shrimp, and several may depend partly on menhaden, so a basic policy question is whether the intense shrimp and menhaden fisheries are now appropriating so much of the production of these species as to reduce the carrying capacity of the system for long-lived species, or at least slow rebuilding of stocks. To determine what Ecosim has to say about this question, we simply shut down the simulated fisheries for red drum, red snapper, and groupers as of 2005, and examined simulated future stock trends.

For all three species (or species complex in the grouper case), the model predicts stock recovery at rates basically the same as those predicted by single-species models, to near the unharvested biomass levels predicted by such models. That is, Ecosim indicates that the shrimp and menhaden fisheries will not in fact impair rebuilding programs for long-lived species. It predicts that, as biomasses of the overfished species rebuild over time, fish will simply adjust foraging times and diet compositions so as to feed more on the wide suite of abundant "forage species" like scaled sardine (*Harengula jaguana* Poey, 1865) and juvenile ladyfish (*Elops saurus* Linnaeus, 1766) that are not as yet heavily exploited. Further, the model predicts that stock rebuilding will not substantially reduce productivity of the shrimp and menhaden stocks, because the larger piscivores apparently only account for a small proportion of the total mortality rate of shrimp and menhaden in the first place and would not generate much higher *M's* even if they were much more abundant.

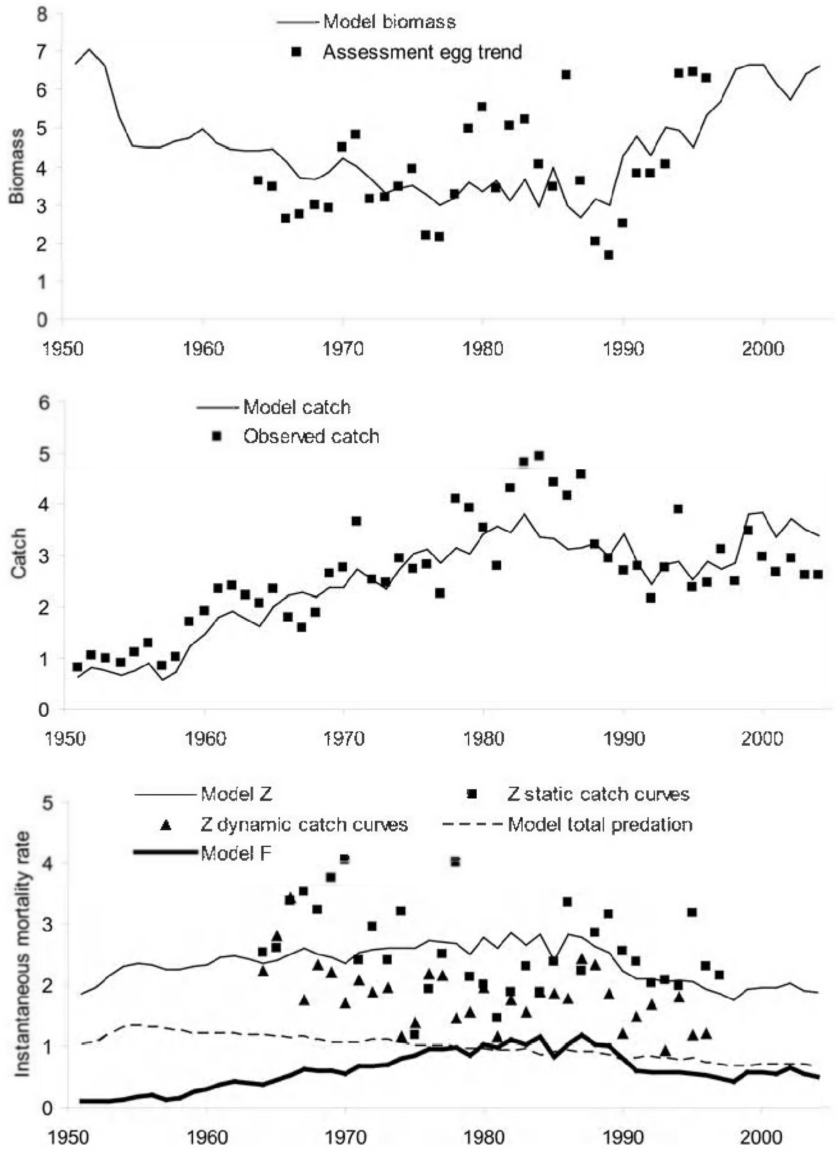

Figure 3. Predicted and observed indicators of model performance for the Gulf of Mexico menhaden stock. Note that growing fishery impact as measured by fishing mortality rate *F* is predicted to have been accompanied by declining predation mortality rates, mainly due to reduction in abundance of coastal sharks.

Development of New Fisheries for Forage Species.—Large demand may develop for small forage fish as feed for developing coastal aquaculture opportunities, for example for bluefin tuna [*Thunnus thynnus* (Linnaeus, 1758)] and cobia [*Rachycentron canadum* (Linnaeus, 1766)]. We simulated development of a fishery for scaled sardine, bay anchovy [*Anchoa mitchilli* (Valenciennes, 1848)], and silver perch

[*Bairdiella chrysoura* (Lacépède, 1802)] (all high biomass groups, see Table 1), to a scale that would cause fishing mortality rates comparable to the current menhaden fishery.

Not surprisingly, Ecosim predicts unequivocally that such a fishery would have devastating impacts on most major piscivores in the system, from red drum to mackerels and red snapper. Ecosim models have generally predicted "bottom-up" effects of fisheries on particular forage species to be relatively weak compared to "top-down" effects of reducing predator abundances on prey mortality rates (Walters et al., 2005), but a forage fishery with such broad impacts would leave few options for piscivores seeking other food supplies.

Reduction of Impacts of the Shrimp Trawl Fishery.—The Gulf shrimp trawl fishery has been an obvious target of demands for improved ecosystem management through reduced by-catches and benthic habitat damage. By-catch reduction in particular is a central demand in plans for rebuilding at least one long-lived fish species (red snapper, see SEDAR 7, 2005, recommendations). During SEDAR 7 assessment reviews, the wisdom of by-catch reduction was questioned by a few reviewers when stock assessment models for red snapper indicated positive recruitment anomalies over recent decades when shrimp by-catch impacts have been greatest.

When we shut down the Gulf shrimp fishery in Ecosim, or at least eliminate its by-catch impacts by creating a new fishery with very low assumed by-catch per unit trawl effort, the outcome is very surprising (Fig. 4). Juvenile survival rates of several long-lived species (red drum, red snapper, groupers) actually decline rather than increase as expected, and productivity of the menhaden stock also declines substantially. Modeled negative impacts are particularly severe for red drum and menhaden. The basic cause of these negative impacts is very simple: Ecosim indicates that shrimp trawling has had a very large negative impact on abundances of some benthic predatory fish, particularly the catfishes. When by-catches are reduced, these species increase severalfold in abundance and cause high predation mortality for a variety of juvenile fish (and older menhaden).

To determine how predictions about shrimp-trawl impact on adult red snapper were influenced by the model-fitting procedure, we performed a sensitivity test in which we fitted the model to time series while estimating different numbers of vulnerability parameters (one per consumer) and spline points for primary-production anomalies. We ran two simulations for each parameter combination, one of them with shrimp trawling stopped from 1990 onward. We compared the biomasses of adult red snapper in the two series of predictions. We found that most fitting trials resulted in parameter estimates that predict adult red snapper would increase after a shrimp-trawl ban, but only few of the combinations indicate a substantial increase; more indicate no or very limited snapper recovery. Most estimation trials indicated a peak in primary production during the 1980s.

We initially dismissed the results from the shrimp-trawl discontinuation scenario as obviously too extreme, but on reflection, it warns us that abundances of many species in the current Gulf ecosystem have developed in the face of massive shrimp trawling, and quite possibly that some species have even benefited from the impacts of that trawling. Catfish are particularly abundant in coastal Florida where inshore trawling has been banned. They are long-lived and as mouth brooders have very low fecundity, so they are likely to have declined drastically in heavily trawled areas. They certainly eat juvenile fishes when they can, and at least one Ecopath model has at-

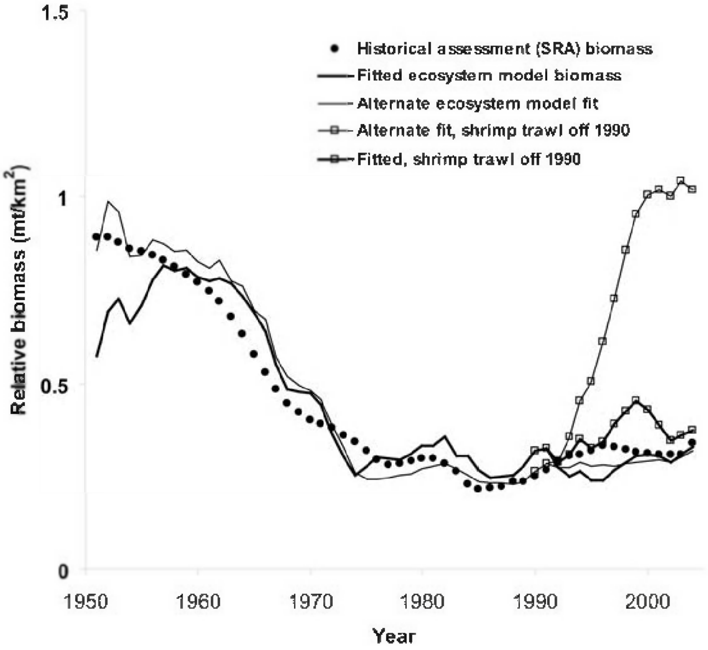

Figure 4. Predicted and observed trends in red snapper adult abundance, under historical fishery impacts and after simulated closure of the shrimp trawl fishery in 1990 ("shrimp trawl off 1990"). Divergent predictions of response to the trawl closure resulted from use of different protocols for choosing which predation-vulnerability parameters to include in fitting the model to historical data.

tributed a high proportion of total menhaden natural mortality to them (J. Carlson, NMFS Panama City, pers. comm.).

Reviews of changes in community structure in shrimp trawl areas since the 1930s (Chesney et al., 2000; Chesney and Baltz, 2001) do not indicate a large decline in catfish abundance, and catfish tend to be distributed farther inshore than juvenile red snapper (Muncy and Wingo, 1983). We can therefore apparently reject the "catfish hypothesis" as a specific reason for failure of by-catch reduction to result in red snapper recovery. Unfortunately, this rejection is not the point; what the Ecosim model has shown us is not that catfish per se are important but that species that have been decreased by trawl by-catch may increase so greatly as to have strong negative impacts on red snapper recovery. Clearly, further, careful analysis of historical by-catch and relative-abundance trend data is needed if we are to identify other species that might play the same role as catfish do in causing the results in Figure 4.

REDUCTION OF THE MENHADEN FISHERY.—Concerns about impact of the Atlantic menhaden fishery on capability of the menhaden to support predators like striped bass [*Morone saxatilis* (Walbaum, 1792)] and about by-catch of sharks in Gulf menhaden purse seining, could prompt ecosystem-scale management policy that would reduce or eliminate the menhaden fishery so as to maximize the value of menhaden as forage for more valued species like mackerels and drum.

Ecosim runs indicate relatively little impact on other species and fisheries of shutting down the menhaden fishery. Apparently, relatively few species really depend on menhaden, so increasing their abundance moderately by removing the fishery would not change the total forage fish "resource" for piscivores substantially. The same argument also holds for mullet, for which a major reason to shut down gillnet fisheries in Florida was concern about its importance as food for predatory fishes; in that case, we cannot see in any available data (or Ecosim runs) indication that substantial increases in mullet abundance have affected growth or survival of their predators.

Discussion

The policy tests reveal a key point about ecosystem models like the one we are developing for the Gulf of Mexico: such models cannot simply be classified as right or wrong, adequate or inadequate in any general way. Instead, the credibility of the model predictions is highly policy-specific. So long as we stick to simple predictions about single-species regulation, e.g., rebuilding overfished stocks, the model is just as credible as its single-species counterparts, because it gives essentially the same stock reconstructions and predictions (both types of models could of course be badly wrong). Only when we step into a policy issue where species interactions, and dynamics of poorly studied "by-catch" species (like catfish), are involved do highly surprising and less credible predictions begin to appear.

Certainly none should take the above predictions about benefits from shrimp trawling for other fisheries at face value; they are based on inference chains that began with untested assumptions about historical impact of trawling on abundance of benthic predators, moved to further untested assumptions about impact of those predators on juvenile (and adult in case of menhaden) survival rates of several species based on very weak diet-composition data and prey-preference assumptions for the benthic predators, and linked both these uncertain effects with other assumptions about population dynamics responses of long-lived species. The model could go badly wrong at any point in such a chain, and other such chains, as yet unrecognized in the model formulation, could be more important. Further, the model obviously does not even account for all species in the Gulf of Mexico coastal ecosystem (nor would obtaining the required parameter estimates to do so ever probably be practical), and some currently "rare" species could show even stronger numerical responses to policy changes like trawl closures than we predict for common and obvious species like catfish. Simply by refitting the model with different protocols for deciding which vulnerability parameters to include in the nonlinear estimation procedure, we were able to obtain good fits to the red snapper data but a prediction that red snapper should recover strongly if the shrimp fishery were reduced (Fig. 4).

In particular, the most critical predictions of change in juvenile mortality rates with changes in predator abundance involve cases where abundant predators could be causing high mortality rates of prey, without those rates being represented as high (or even practically measurable at all) proportions of the predator diets. For such interactions, we may have no practical way to determine whether the interaction is actually important other than to do some direct manipulation of predator abundance, then determine whether net juvenile survival and recruitment rates respond. This problem raises a key point: to test the Ecosim predictions about changes in benthic predator abundance due to trawling, and impact of benthic predators on other species, the best strategy may be to develop spatial comparisons (trawled vs. untrawled areas) rather than to rely on time-series model fitting. Indeed, the deliberate use of areas closed to trawling (MPAs) as a tool for investigating trawl effects on community structure may be worth considering, entirely independent of the value of such protected areas for marine habitat and biodiversity.

Given that development of a "complete" model for any ecosystem as large and complex as the Gulf of Mexico will probably never be possible, and that the predictions of any practical model will therefore be highly suspect, should we simply abandon such modeling efforts entirely, in favor of intuitive management prescriptions (e.g., trawling must be bad because it kills fish, so reduce its impact) or large-scale management experiments? We think the answer is a resounding no. The models have at least two key values, even when most of their parameters are highly uncertain. First, they allow us to play "policy games," such as the shrimp-trawl closure simulation, and thereby to screen policy options for possible efficacy and possible pitfalls such as a catfish population explosion. Second, they can be used as the starting point for further, precisely focused research and modeling on interactions that appear to have potential for producing surprising effects. The "catfish hypothesis" has clearly indicated that we must understand more about population dynamics, diet compositions, and impacts on other fish species of species like catfish that have been affected by trawling before proceeding to implement policies for "obviously" beneficial reduction of trawl by-catches. Armed with the warning that Ecosim has provided, we should now find it relatively easy to do the more focused analysis of catfishes (and other predatory fish that have been affected by trawling) to determine whether they are indeed depressed in abundance, do indeed eat enough of other valued species to be of concern, and are likely to respond in dangerous ways to by-catch reduction. Doubtless, we will uncover more such critical and well-defined uncertainties as we play further with the model, and as we challenge it with more questions both about its input data and about its predictions of response to other policy options.

A really important benefit from the model development to date has been provision of a "straw man" starting point for pulling together and documenting parameter estimates from a wider variety of sources than have been accessible to us, vetting those data through careful review processes like SEDAR, and systematically exploring policy options and sensitivity of predictions to uncertain data in workshop processes again similar to the SEDAR process. The Gulf of Mexico Fishery Management Council has supported two preliminary workshops aimed at starting such an ongoing model-development and policy-testing process, and we have every reason to believe that the process will continue.

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