A 'STRAW-MAN' ECOPATH MODEL OF THE MIDDLE ATLANTIC BIGHT CONTINENTAL SHELF, UNITED STATES

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ABSTRACT

A considerable amount of information exists about the biological communities of the 'Middle Atlantic Bight' continental shelf (United States), and a number of scientific efforts have summarized and integrated various components of this system. A constant challenge for scientists, managers, and policy makers is that natural complexities and uncertainties can render the usefulness of food web models difficult to gauge, though research groups from the region are working to meet this challenge. No approach can enable complete understanding of an ecosystem, but new advances in modeling tools can help describe the interactions within marine food webs (and ecosystems). These cohesive descriptions of the changing states and dynamics of food webs are transparent and relatively accessible to all interested parties. A preliminary model of the Middle Atlantic Bight continental shelf food web was constructed using Ecopath with Ecosim, as a way to complement current ecological characterizations. The current model is considered a preliminary 'straw-man,' and was built as a focal point for future refinements. The defined area covered by this model extends from the SE tip of Cape Cod, Massachusetts in the north to Cape Hatteras, North Carolina in the south, and from the intertidal (and the entrance of estuarine systems) to the shelf break at the 200 m isobath. This preliminary model was designed to characterize the four years from 1995 to 1998.

INTRODUCTION

The continental shelf ecosystems adjacent to the east coast of the United States are among the best studied marine ecosystems in the world. Given the importance of this region for supporting fisheries, combined with availability of broad ecological information, it is not surprising that food web models have been constructed and employed to characterize particular areas in the region.

A number of ecosystem models (or multi-species models) have been constructed for systems within the marine areas off the Northeastern United States (Brown *et al.*, 1976; Cohen *et al.*, 1982; Murawski, 1984; Sissenwine *et al.*, 1984; Overholtz and Tyler, 1986; Fogarty *et al.*, 1991; Overholtz *et al.*, 1991; Link, 1999). This body of work, along with overarching scientific programs such as the food web dynamics program of the Northeast Fisheries Science Center at Woods Hole, Massachusetts (see Link and Almeida, 2000) and previous programs such as the Marine Resource Monitoring and Assessment Program (MARMAP), represent a good framework for organizing a broad array of information on fisheries, diet compositions, biomasses, and other biological characteristics collected during the last few decades in the region.

The Southeast Area Monitoring and Assessment Program (SEAMAP) and the South Atlantic Bight Recruitment Experiment program (SABRE) are other sources of good biological information with some relation to the Middle Atlantic Bight. Numerous up-to-date assessments of fishery and marine mammal stocks in the marine areas off the Northeastern United States are also rich sources of information for piecing together a cohesive picture of the system as a whole (see Table 1 for these citations). Some other sources are also available for putting stock changes into historical context (e.g., Reeves *et al.,* 1999).

The area of focus for the present modeling effort is the Middle Atlantic Bight continental shelf, here defined as extending roughly from Cape Cod Massachusetts (excluding George's Bank) to Cape Hatteras, North Carolina.

The previous modeling efforts in this region have been a crucial aspect of efforts to synthesize the vast information collected in these programs, as well as information that has accumulated during the last century. For example, whole-system approaches to fishery management dilemmas have been recently undertaken (Fogarty and Murawski, 1998; Overholtz *et al.,* 1999, 2000). Unlike some past approaches, this new generation of whole-system analyses has the potential to be transparent and accessible to researchers and non-researchers alike.

Newly emerging approaches to whole-ecosystem trophic modeling, such as Ecopath with Ecosim, now enable scientists to simultaneously simulate the potential direct and indirect effects of human activities on these naturally dynamic systems (Pauly *et al.,* 2000). In this approach, a preliminary model must be constructed and subjected to refinement and criticism through several iterations, and on several levels, before dynamic Ecosim analyses can be conducted in a useful enough manner to support fisheries and conservation policy decision-making.

The goal of the work documented in the present contribution was to construct a 'straw-man' Ecopath model using some of the best information available, and which can be evaluated in the context of past models and newly emerging information. This exercise was conducted to provide an operational framework for collaborative refinement of this 'straw-man' model in the near future. It is not the purpose of this paper to explain the Ecopath with Ecosim approach in detail, or to discuss particular simulations or analyses that will be possible once the model has been constructed and refined (but see other contributions in this volume).

METHODS

Ecopath models are static descriptions of biotic flows in food webs. They include all biotic components of an ecosystem, and the most typical currency used is biomass (in wet weight). Polovina (1984) originally developed the Ecopath approach for application to the coral reefs of the French Frigate Shoals.

Since then, a variety of dynamic capabilities have been added to Ecopath with Ecosim (e.g., Christensen and Pauly, 1992; Walters *et al.,* 1997; Walters *et al.,* 1999; Christensen *et al.*, 2000; Pauly *et al.*, 2000). These dynamic simulation capabilities allow explorations of the potential effects of human activities (e.g., fisheries and other disturbances or stressors) on the biological components in a system (Pauly *et al.*, 2000), and are thus a key reason for constructing Ecopath models. However, these dynamic approaches were not discussed here. Scores of applications of Ecopath with Ecosim can be found at *www.ecopath.org*.

The Ecopath foundation

The Ecopath 'master equation' (Equation 1) states that the net production of a functional group equals the total mass (or energy) of that group that is removed by predators and fisheries plus the net biomass accumulation in the group plus the net migration of the group's biomass plus the mass flowing to detritus. This master equation also indicates the basic parameters needed to construct an Ecopath model.

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \Sigma\, B_j \cdot (Q/B)_j \cdot DC_{ji} + BA_i + NM_i \quad \ldots 1)$$

B_i and B_j are biomasses of prey ($_i$) and predators ($_j$) respectively;
P/B_i is the production/biomass ratio, equivalent to total mortality (Z) in most circumstances (Allen, 1971);
EE_i is the ecotrophic efficiency; the fraction of the total production of a group that is utilized in the system;
Y_i is the fisheries catch per unit area and time (i.e., $Y = F*B$);
Q/B_j is the food consumption per unit biomass of j; and
DC_{ji} is the contribution of i to the diet of j;
BA_i is the biomass accumulation of i (positive or negative);
NM_i is the net migration of i (emigration less immigration).

This equation describes the law of conservation of mass or energy, or the inescapable 'truth' of thermodynamic *continuity* in a system of energy or biomass flows. This law must apply to dynamic systems as well as 'steady-states,' and it must also apply to each component of such systems (i.e., functional groups). Representative estimates of the parameters are derived for each functional group using sums or appropriately weighted estimates of functionally aggregated species (also see Okey and Pugliese, and other contributions in this volume for further explanation of Ecopath basics).

Defining the system

The Middle Atlantic Bight (MAB) is generally considered to extend from Cape Cod Massachusetts in the north, to Cape Hatteras, North Carolina, in the south; and the seaward boundary is the shelf slope break (Pearce, 2000). These geographic boundaries are conventionally used because they also delineate oceanographic, ecological, and other physical boundaries. For the purposes of the present Ecopath model, the northern boundary of the area is a line extending from the Chatham lighthouse on the elbow of Cape Cod extending southeast along the Great South Channel to a point on the shelf break south of George's bank (69° W Longitude, 40.25° N Latitude). The southern boundary is the latitude of Cape Hatteras. The shallow edge of the area is the upper intertidal and the entrance of estuarine systems; and the deeper edge is the 200 m isobath, which delineates the shelf break. The area covers approximately 111,200 km^2. The preliminary MAB model is designed to characterize four years during in the late 1990s (1995-1998).

Assembling the list of species

Four major sources were used to assemble the list of over 400 species included in the Ecopath model of the Middle Atlantic Bight continental shelf system: (1) the National Marine Fisheries service (NMFS) recreational fish landings for the eight states; (2) NMFS commercial fish landings for the eight states; (3) a list previously developed for the South Atlantic States continental shelf (Okey and Pugliese, this volume); and (4) The NMFS marine mammal stock assessments (NMFS, 2000). In addition, two sea turtle web resources were consulted for information on turtles: *www.nmfs.noaa.gov/prot_res/PR3/ Turtles/turtles.html* and *www.cccturtle.org/ species.htm*.

Aggregation of functional groups

The same approach was taken to aggregate all species in this continental shelf ecosystem list into 55 functional groups (as also used by Okey and Pugliese, this volume). These preliminary groups were chosen based on several criteria, the food web of 75 groups presented by Link (1999) was used as a general guide. Some of the original 75 groups were aggregated while some others were added. Groups managed under a federal fishery management plan and fish groups for which commercial or recreational landings exceeded 200 tonnes in any of the states within each area were included as explicit groups in the model. After identification and addition of these explicit groups, species lists representing the remaining components of the system were aggregated into functional groups based on knowledge of natural history and diet. The functional group aggregation in this ‘straw-man’ model is intended as preliminary. It was considered that refining the structure (aggregation) of the system would provide ample room for debate, and that a framework for broad collaboration might be the best approach for refining the model in the future. Some preliminary suggestions for restructuring the current ‘straw-man’ model are presented in the Discussion.

Sources of the basic input parameters

The ‘basic input parameters’ of the Ecopath model are biomass (B), the ratio of production to biomass (P/B), the ratio of consumption to biomass (Q/B), and diet composition. A variety of sources were conducted to derive estimations for these basic input parameters, and these sources are shown in Table 1. Other basic parameters include biomass accumulation, migration, the ratio of unassimilated to consumed food, and the ratio of production to consumption (P/Q).

Biomass estimations

The biomass of 26 out of the 55 groups in the straw-man MAB model were estimated as inputs of the model; biomasses for the rest of the groups in the model were estimated by the Ecopath routine. Most of the 26 biomass input estimations were based on a suite of up-to-date population assessments in the region (Table 1). Most of these biomasses applied to stocks with ranges larger than the Middle Atlantic Bight, and were thus adjusted by assumed conversion factors representing an estimated proportion of the assessed stock within the MAB model area. These conversion factors are probably a large source of error. Future iterations of this model should include rigorous approaches for estimating relative proportion of assessed stocks occurring within the modeled area during a given year. Estimations of stock size in marine mammal assessments were converted to biomasses using average body mass estimations from Trites and Pauly (1998), and other sources.

P/B estimations

A variety of sources were consulted during the derivations of P/B values for the 55 functional groups (Table 1), and different approaches were used for these derivations. Some studies directly measured production rates of the organisms in question. Values estimated from within ecologically similar systems were preferred when available. Another common approach was to use an estimate of total mortality as a proxy for P/B. This method is based on Allen (1971): the production rate (P/B) equals the total mortality of a population, and the total mortality equals the sum of natural mortality and fishing mortality ($P/B = Z = M + F$). This relationship should be reliable when a species, or functional group, spends its whole life cycle within the system of interest, and accurate mortality estimates are available. In such an open and dynamic system as the Middle Atlantic Bight, these assumptions do not apply to all functional groups. In cases of aggregated functional groupings, P/B values for individual species were weighted based on the relative biomass of the species in the functional group, or a P/B estimate from representative species were used.

Table 1. Sources of basic parameter estimates. The values used as inputs in the 'straw-man' Middle Atlantic Bight shelf model were derived from these sources based on their application to the defined system, rather than being simply extracted.

Group name	**Biomass ($t \cdot km^{-2}$)**	**P/B ($year^{-1}$)**	**Q/B ($year^{-1}$)**	**Diet composition**
Billfishes	-	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Bluefish	Shepherd (2000a)	Shepherd (2000a)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Tunas	Heymans (this volume)	Heymans (this volume)	Heymans (this volume)	Mackinson (2000)
Dolphins & porpoise	NMFS (2000)	Matkin and Hobbs (1999b)	Kastelein *et al.* (1997); Matkin & Hobbs (1999b)	
Seals	Payne and Selzer (1989); NMFS (2000)	Banse & Mosher (1980); Trites & Pauly (1998); Heymans (this volume)	Hammill & Stenson (2000); Sissenwine (1987) in Heymans (this volume)	from Heymans (this volume)
Goosefish	-	Froese & Binohlan (2000); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Coastal sharks	SEAMAP-SA / SCMRD (2000)	Sissenwine (1987); Heymans (this volume)	Acosta *et al.* (1998)	Mackinson (2000)
Marine birds	-	Acosta *et al.* (1998)	Powers & Backus (1987) in Heymans (this volume)	Powers & Backus (1987) in Heymans (this volume)
Striped bass	Shepherd (2000b)	Froese & Binohlan (2000); Froese & Pauly (2001); NMFS (2000)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	Stevens (1966)
Weakfish	-	Froese & Binohlan (2000); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Snapper / grouper	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Baleen whales	Dolphin (1987); NMFS (2000)	Matkin and Hobbs (1999a)	Dolphin (1987)	From Matkin and Hobbs (1999a)
Jacks	-	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Spiny dogfish	Sosebee (2000a)	Sosebee (2000a); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Benthic piscivores	Heymans (this volume)	Mackinson (2000)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Black seabass	-	Froese & Binohlan (in press.); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Demersal piscivores	-	Sissenwine (1987) and Heymans (this volume)	Sissenwine (1987); Martini *et al.* (1997) in Heymans (this volume)	Mackinson (2000)
Octopods	-	Buchan and Smale (1981)	Guerra (1979) in Pauly *et al.* (1993)	Okey (2000)
Cods and hakes	Mayo and O'Brien (2000), Brown (2000), Brodziak (2000a,b), Sosebee (2000b, 2000c)	Cohen *et al.* (1982); Heymans (this volume)	Cohen *et al.* (1982); Froese & Pauly (2001); Heymans (this volume); but see Durbin *et al.* (1983)	NMFS (unpublished data)
Redfish	Heymans (this volume)	Cohen *et al.* (1982); Sissenwine (1987)	Cohen *et al.* (1982); Sissenwine (1987)	Konchina (1986); Vinogradov (1984)
Lg. pel. planktivores	-	Sissenwine (1987)	Mackinson (2000)	NMFS (unpublished data)
Mackerel	Overholtz (2000a)	Cohen *et al.* (1982); Sissenwine (1987)	Cohen *et al.* (1982); Sissenwine (1987)	NMFS (unpublished data)
Drum / croaker	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Benth. invert. eaters	-	Mackinson (2000)	Mackinson (2000)	NMFS (unpublished data for sea raven and longhorn sculpin)
Butterfishes	SEAMAP-SA / SCMRD (2000)	Froese & Binohlan (2000); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Squid	-	Cohen *et al.* (1982); Sissenwine (1987)	Cohen *et al.* (1982); Sissenwine (1987)	NMFS (unpublished data)
Atlantic salmon	-	Froese & Binohlan (2000); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	Values inspired by Keeley and Grant (1997)

Table 1 continued

Group name	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	Diet composition
Atlantic menhaden	-	Sissenwine (1987); Heymans (this volume)	Sissenwine (1987); Froese & Pauly (2001)	Vinogradov (1984)
Forage fish	Overholtz (2000b)	Sissenwine (1987); Heymans (this volume)	Cohen *et al.* (1982); Sissenwine (1987); Stone & Jessop (1994)	NMFS (unpublished data)
Dem. planktivores	-	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Tilefish	Nitschke (2000)	Froese & Binohlan (2000), Froese & Pauly (2001), Nitschke (2000)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	Sierra *et al.* (1994)
Flounders	Hendrickson (2000a,b), Terceiro (2001), Cadrin (2000), Wigley (2000), Nitschke *et al.* (2000)	Cohen *et al.* (1982); Heymans (this volume); Sissenwine (1987)	Cohen *et al.* (1982); Sissenwine (1987); but see Huebner & Langton (1981)	NMFS (unpublished data)
Euphausiids	-	Tanasichuk (1998)	-	T.A. Okey (estimation)
Scup	-	Froese & Binohlan (2000); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Lobsters	-	Arreguín-Sánchez *et al.* (1993)	Arreguín-Sánchez *et al.* (1993)	adapted from Martínez (2000)
Ocean pout	-	Froese & Binohlan (2000); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	NMFS (unpublished data)
Stomatopods	-	Meyer & Caldwell (2000)	Meyer & Caldwell (2000)	Meyer & Caldwell (2000)
Dem. invert. eaters	-	Sissenwine (1987) and Heymans (this volume)	Sissenwine (1987)	Mackinson (2000)
Rays and skates	-	Sosebee (2000d), Froese & Binohlan (2000), Froese & Pauly (2001)	Heymans (this volume)	NMFS (unpublished data)
Jellies	-	Okey *et al.* (1999)	Graham (2000)	Okey *et al.* (1999)
Mysids	-	Azeiteiro et al. (1999)	-	T.A. Okey (estimation)
Macrozooplankton	Heymans (this volume)	Cohen *et al.* (1982); Sissenwine *et al.* (1984); Sherman *et al.* (1987)	-	Sissenwine *et al.* (1984)
Crabs	-	Ehrhardt and Restrepo (1989)	Arreguín-Sánchez *et al.* (1993)	Bundy (2000)
Spot	-	Froese & Binohlan (2000); Froese & Pauly (2001)	Palomares & Pauly (1989, 1999); Froese & Pauly (2001)	Adams (1976)
Shrimp	-	Parrack (1981); Arreguín-Sánchez *et al.* (1993); Okey & Nance (2000)	Arreguín-Sánchez *et al.* (1993)	Bundy (2000)
Echonoderms	Steimle (1987) and Theroux and Grosslein (1987)	Opitz (1993)	Pauly *et al.* (1993) in Heymans (this volume)	Okey (2000 a)
Sessile epibenthos	-	Odum and Odum (1955) and Sorokin (1987) in Opitz (1993)	Wilkinson (1987); Sorokin (1987) in Opitz (1993)	Okey (2000 b)
Polychaetes	-	Pagliosa Alves and Lana (1998)	-	T.A. Okey (estimation)
Small crustaceans	-	Sanders (1956), Arreguín-Sánchez *et al.* (1993)	Arreguín-Sánchez *et al.* (1993)	T.A. Okey (estimation)
Bivalves	Lai and Rago (2000)	Arnold et al. (2000)	Guénette (1996)	Arnold et al. (2000)
Microzooplankton	Heymans (this volume)	Banse and Mosher 1980	-	Sissenwine *et al.* (1984)
Phytoplankton	Cura (1987), O'Reilly *et al.* (1987)	O'Reilly *et al.* (1987); Cahoon and Cooke (1992)	n/a	n/a
Macrophytes	-	Luning (1990)	n/a	n/a
Microphytobenthos	-	Cahoon and Cooke (1992)	n/a	n/a
Detritus	Heymans (this volume)	n/a	n/a	n/a

Q/B estimations

Sources of Q/B estimates are listed in Table 1. The ratio of annual consumption to biomass (Q/B) for a functional group is the annual food ration for that group relative to its average annual standing biomass. The most common approach used for estimating Q/B for a given functional group in the Middle Atlantic Bight Ecopath model is based on an empirically based equation originally derived, and later refined, by Palomares and Pauly (1989, 1999). This approach is used to estimate Q/B based on a species' maximum or asymptotic weight (W_{inf}), the mean ambient water temperature, the food type, and the tail aspect ratio, which indicates a species' metabolic characteristics. This approach applies only to fishes, and a 'Q/B calculator' in FishBase, the global database on fishes (Froese and Pauly, 2001), can be used to make these estimations for individual fish species. Representative averages of these estimations for the species in a functional group were obtained by weighting the species-specific estimates by relative consumption or biomass of each species. Other approaches for estimating Q/B include direct measurement in the context of empirical studies, and these were usually the sources of invertebrate Q/B estimations. I incorporated Q/B estimations from the empirically based relationship described above, from empirical studies, and sometimes from identical or similar functional groups from similar Ecopath models.

Sources of diet composition information

The Middle Atlantic Bight Ecopath model features the extensive diet composition information gathered during the last 28 years during the food web dynamics program of the Northeast Fisheries Science Center, at Woods Hole, Massachusetts (NMFS, unpublished data; Link, 1999; Link and Almeida, 2000). This information consists of species-specific diet compositions collected from myriad stomachs analyzed in this program (diet compositions generated for most species were based on a minimum of 250 stomachs). These data were adapted to the functional groupings chosen for this model using an Excel spreadsheet. Other sources of diets used in this preliminary model are shown in Table 1.

Source of fisheries information

The commercial fisheries catch data from the NMFS database (*www.st.nmfs.gov/st1/*) were used to estimate the average annual commercial and recreational fisheries landings in Rhode Island, Connecticut, New York, New Jersey, Delaware, Maryland, and Virginia during the late 1990s (1995-1998). Twenty five percent of the Massachusetts landings for each species were also included. This is an arbitrary proportion used for convenience during this 'straw-man' phase of model development. In the future, a rigorous method should be developed to assign a more correct proportion of the Massachusetts fishing effort to the defined Middle Atlantic Bight system. Discards were taken to be 20% of the landings across-the-board, and these 'place-holder' discard values were entered in the discard interface of EwE.

Balancing the model

The initial input parameters of the Middle Atlantic Bight Ecopath model comprised a model that was remarkably close to being thermodynamically balanced at the outset. When the model was first run to calculate basic parameters, thermodynamic discontinuities ('unbalanced' groups) are indicated when ecotrophic efficiency values exceed 1.0 for a particular group. This means the energy produced by that group is exceeded by the predatory demand on that group (including fishing mortality). Such a group is brought back into energy continuity ('balance') by either decreasing predatory consumption on that group through adjustment of consumption rates (Q/Bs) or proportions (diet compositions), or by upwards adjustments of the biomass of the group or its production rate (P/B). Alternately, rates of production to consumption (P/Q), or growth efficiency, of predators can be adjusted. Such adjustment options pre-suppose uncertainty in the parameters. Thus, the best way to 'balance' an Ecopath model is to develop a systematic approach to prioritizing estimates based on data quality. Such an approach is best implemented by a collaboration of experts who 'negotiate' with each other (with a mediator/coordinator) to determine which parameters to adjust first or most (Okey and Pauly, 1999).

The designers of the Ecopath approach advise users to minimize cannibalism within functional groups to ensure useful estimations of system dynamics. The best approach to minimizing cannibalism is to ensure that groups are disaggregated in a functional sense, such that cannibalism is naturally minimized.

The second step in Ecopath model balancing is to examine the consumption rates upon each unbalanced group, beginning with the most unbalanced group. In cases where the higher rates of consumption were not supported by robust diet composition information, the diets of predators are appropriately adjusted to decrease these consumption values. However, in the case of the Middle Atlantic Bight model, the diet compositions were considered to be somewhat of a cornerstone of the model. Thus, the second step for balancing the MAB model was to carefully re-examine the assumptions behind the biomass estimates, which were considered less reliable than the diet compositions. Adjustment of biomass estimates was used liberally during this initial balancing procedure because many of the initial biomass estimates were considered to be placeholders.

Sixteen of the groups were out of thermodynamic balance the first time the 'basic parameters' were estimated, as in the model of the South Atlantic States continental shelf (SAS). The MAB model, however, currently has 55 functional groups, whereas the SAS model has only 42 groups. Thus, the present model had 29% of the groups initially unbalanced, compared with 38% of the groups in the SAS model. The ecotrophic efficiency of the unbalanced groups in the MAB model ranged from 1.06 to 215, and the mean of the EE values for these unbalanced groups was 22.9 ± 13.7 (standard error). This indicates more of an overall imbalance than in the SAS model (range: 1.09 to 27.07; mean: 5.89 ± 1.54 SE). Crabs (EE = 215) and Shrimps (EE = 65.25) (followed by benthic invertebrate eating fishes; EE = 47.42) were the main reason the imbalance in the initial MAB model exceeded that of the initial SAS model, and these three components (and predation on them) were modified considerably during model balancing.

RESULTS AND DISCUSSION

An initial attempt was made to construct a well-articulated model of the Middle Atlantic Bight food web, and the current model contains 55 functional groups. Table 2 shows the basic parameters of the Middle Atlantic Bight continental shelf model. Summary statistics for the system are presented in Table 3, and the sources of the basic parameters are shown in Table 1. The diet composition matrix is presented in Table 4.

This preliminary model of the Middle Atlantic Bight continental shelf was constructed to provide a new quantitative framework for the refinement of the model's input parameters so that an up-to-date, cohesive view of both the structure and the dynamics of the whole marine ecosystem can emerge. Notwithstanding the natural limitations of broad-system modeling approaches, this 'straw-man' model has the potential to enable a better understanding of this important ecosystem for students, scientists, and other stakeholders. This approach is intended to complement, rather than replace, other assessment and management tools currently in use. It is a tool that can help operationalize the new era of ecosystem-based management.

The model is presented as a focal point for scrutiny and criticism of input parameters so that an improved understanding of the system can emerge. Experts in the various biotic components of the system can be identified and assembled into a coordinated and collaborative refinement strategy. Refinement of the 'straw-man' MAB model by a working group of experts ought to be coordinated such that a central copy of the model is maintained. This process should include several iterations of review and refinement, but a practical sunset for the process should be identified so that the model can be applied to questions of interest using the dynamic simulation routines of Ecopath with Ecosim (Walters *et al.,* 1997; Walters *et al.,* 1999; Pauly *et al.*, 2000).

Improvements to the model should begin with the broadest issues, such as the overarching issues of system definition and aggregation of functional groupings (the overall model structure). Species should be aggregated based on functional rather than taxonomic similarity, but the structure of the model can be adjusted according to the interest of the investigators. Thus, a particular sub-system of the model can be 'broken out' if the questions of interest relate to the articulation of that sub system. For example, the current model contains a variety of aggregated groups for which an adept researcher might suggest disaggregating. These groups include skates and rays, cods and hakes, flounder, drum and croaker, snapper and grouper, forage fishes, benthic invertebrate eaters (e.g., sculpins and sea robins), dogfishes, squid, jellies, shrimps, crabs, sessile epibenthos, benthic infauna, bivalves, gastropods.

Functional groupings need not be taxonomically consistent; biomass and taxonomic lumping vs. splitting can vary widely among functional groups. The only strong recommendation for aggregation is that the species (or life stages) in a given functional group be reasonably similar in functional terms. System definition and functional group aggregation issues are centrally important for model construction and behavior. Given the complexity of real world ecosystems, considerable effort should be invested in these two important issues.

Table 2. Basic parameters of the 'straw-man' Ecopath model of the Middle Atlantic Bight continental shelf. Values in bold have been calculated with the Ecopath software; other values are empirically based inputs, or values that were adjusted from empirically based values during balancing. The omnivory index, OI, represents the uncertainty in the trophic level estimate.

Group name	Trophic level	OI	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE
Billfishes	**4.5**	**0.248**	**0.014**	0.44	5.29	0.900
Bluefish	**4.5**	**0.104**	0.083	0.61	4.60	**0.996**
Tunas	**4.5**	**0.229**	0.060	0.40	4.60	**0.996**
Dolphins & porpoise	**4.4**	**0.061**	0.079	0.10	27.00	**0.000**
Seals	**4.4**	**0.194**	0.002	0.25	3.10	**0.000**
Goosefish	**4.4**	**0.141**	**0.504**	0.35	3.10	0.850
Coastal sharks	**4.3**	**0.351**	0.104	0.43	4.18	**0.878**
Marine birds	**4.3**	**0.173**	0.028	0.10	76.18	**0.000**
Striped bass	**4.3**	**0.235**	0.222	0.13	1.40	**0.964**
Weakfish	**4.3**	**0.143**	**0.044**	0.98	3.50	0.950
Snapper / grouper	**4.2**	**0.198**	0.339	0.70	6.76	**0.921**
Baleen whales	**4.2**	**0.130**	0.195	0.05	10.90	**0.000**
Jacks	**4.2**	**0.108**	**0.051**	0.56	9.20	0.950
Spiny dogfish	**4.2**	**0.262**	**0.586**	0.18	4.77	0.950
Benthic piscivores	**4.2**	**0.741**	0.073	0.40	9.85	**0.972**
Black seabass	**4.0**	**0.367**	**0.055**	0.74	3.60	0.850
Demersal piscivores	**4.0**	**0.321**	**1.479**	0.55	4.00	0.990
Octopods	**3.9**	**0.222**	**0.084**	3.10	7.30	0.950
Cods and hakes	**3.9**	**0.351**	0.550	0.65	2.58	**0.987**
Redfish	**3.8**	**0.269**	0.235	0.26	3.00	**0.989**
Lg. pel. planktivores	**3.7**	**0.060**	0.591	0.88	11.52	**0.700**
Mackerel	**3.7**	**0.247**	6.000	0.43	4.30	**0.749**
Drum / croaker	**3.6**	**0.343**	0.361	0.47	7.34	**0.906**
Benth. invert. eaters	**3.5**	**0.292**	**0.784**	1.73	13.57	0.980
Butterfishes	**3.5**	**0.190**	0.080	2.20	5.50	**0.608**
Squid	**3.5**	**0.208**	**2.533**	1.70	7.00	0.990
Atlantic salmon	**3.4**	**0.166**	**0.004**	0.74	7.14	0.900
Atlantic menhaden	**3.4**	**0.130**	**2.871**	1.55	31.40	0.990
Forage fish	**3.4**	**0.507**	8.000	1.50	5.00	**0.966**
Dem. planktivores	**3.3**	**0.111**	**0.068**	2.60	10.00	0.990
Tilefish	**3.3**	**0.151**	0.035	0.42	4.10	**0.923**
Flounders	**3.3**	**0.308**	1.000	0.60	4.10	**0.861**
Euphausiids	**3.3**	**0.295**	**0.807**	17.00	**134.92**	0.950
Scup	**3.3**	**0.162**	**0.013**	1.32	5.50	0.950
Lobsters	**3.2**	**0.359**	**1.257**	1.20	8.20	0.950
Ocean pout	**3.2**	**0.173**	**4.176**	0.50	1.80	0.950
Stomatopods	**3.1**	**0.811**	**0.151**	1.34	7.43	0.950
Dem. invert. eaters	**3.1**	**0.530**	**6.515**	0.76	5.02	0.990
Rays and skates	**3.1**	**0.749**	**1.182**	0.47	3.17	0.900
Jellies	**3.1**	**0.215**	**0.068**	18.25	80.00	0.900
Mysids	**2.8**	**0.336**	**5.429**	2.57	**17.13**	0.950
Macrozooplankton	**2.7**	**0.202**	51.690	7.00	**21.87**	**0.452**
Crabs	**2.6**	**0.402**	**3.125**	1.38	8.50	0.950
Spot	**2.5**	**0.388**	**0.043**	1.82	19.30	0.950
Shrimp	**2.4**	**0.399**	**0.912**	4.00	15.00	0.990
Echonoderms	**2.3**	**0.234**	8.400	1.20	3.70	**0.657**
Sessile epibenthos	**2.2**	**0.192**	**9.728**	0.80	9.00	0.950
Polychaetes	**2.1**	**0.126**	**9.354**	4.08	**27.20**	0.950
Small crustaceans	**2.1**	**0.109**	14.100	5.08	21.52	**0.744**
Bivalves	**2.0**	**0.012**	19.664	1.22	23.00	**0.814**
Microzooplankton	**2.0**	**0.000**	25.000	40.00	**125.00**	**0.985**
Phytoplankton	**1.0**	**0.000**	107.311	88.00	-	**0.387**
Macrophytes	**1.0**	**0.000**	**7.389**	5.00	-	0.700
Microphytobenthos	**1.0**	**0.000**	68.000	55.57	-	**0.078**
Detritus	**1.0**	**0.000**	155.700	-	-	**0.053**

Table 3. Basic summary statistics for the 'straw-man' Ecopath model of the Middle Atlantic Bight continental shelf. Values are expressed in wet weight.

Parameter	Value	Units
Sum of all consumption	5,912	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all respiratory flows	2,555	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all flows into detritus	11,353	$t \cdot km^{-2} \cdot year^{-1}$
Total system throughput	30,581	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all production	14,847	$t \cdot km^{-2} \cdot year^{-1}$
Calculated total net primary production	13,259	$t \cdot km^{-2} \cdot year^{-1}$
Net system production	10,703	$t \cdot km^{-2} \cdot year^{-1}$
Total biomass (excluding detritus)	371	$t \cdot km^{-2}$
Total catches	4.2	$t \cdot km^{-2} \cdot year^{-1}$
Mean trophic level of the catch	3.3	--
Gross fishery efficiency (catch/net p.p.)	0.00032	--
System omnivory index	0.254	TL units
Total primary production/total respiration	5.2	--
Total primary production/total biomass	35.7	$year^{-1}$
Total biomass/total throughput	0.012	$year^{-1}$
Connectance index	0.205	--

A powerful aspect of the current approach, is that the 'straw-man' Ecopath model of the Middle Atlantic Bight can be modified easily according to suggested changes of basic input parameters. Re-aggregation of an existing model can be more challenging because the entire diet matrix must be re-visited and adjusted accordingly. Nevertheless, functional group disaggregation can be straightforward. Disaggregation of subwebs of interest should coincide with aggregation of other subwebs in the system if it is desired to limit the number of groups to a reasonable number (e.g., <50). A collaborative group of experts could thus aggregate groups of 'low interest' while disaggregating groups of 'high interest' in order to address a particular set of questions. Nevertheless, Ecopath with Ecosim can now be used to construct highly articulated models. For example, a food web with 81 groups (e.g., Link 2002) or more can be characterized using this approach.

Real world food webs are profoundly complex (Polis, 1991). Attempting to construct models of food webs for which considerable information exists is thus a deeply challenging task if the goal is to produce a useful representation of that system. Several researchers have argued or implied that the extent to which a food web is articulated in a model appears to strongly influence the types of behavior that a dynamic model exhibits (Polis, 1994; also see Paine, 1988 and Cohen *et al.,* 1993). The challenge of constructing well-articulated models of relatively well-known systems underscores the potential of simpler models to mislead (i.e., simpler models or less well-known systems). This issue can be mitigated, however, by framing the subsystems, or the aggregation regime, with particular and explicit hypotheses.

Once aggregation issues are resolved, suggested improvements should then proceed to the scrutiny, refinement, and tuning of specific parameter estimates by assigning specialists to focus on particular groups with which they have expertise. Issues of these types underscore the need for the development of a coordinated and collaborative refinement strategy that would account for suggestions and 'refinement negotiations' in a transparent and efficient manner. Biomass estimations are the particular weak point of the present straw-man model. Fully 29 out of 55 biomass estimates in this model were estimated using the Ecopath software. These output values represent the 'system need' for minimal biomasses estimates for those particular groups, based on consumption demand on those groups relative to biomass and production rates. This calculation by the Ecopath software can be reasonably accurate when the biomasses of only a few groups are left blank, but useful 'realism' can

Table 4. Diet composition of components of the Mid-Atlantic Bight model.

Prey \ Predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
1 Billfishes	0.004															
2 Bluefish		0.073														
3 Tunas	0.038		0.02													
4 Dolphins & porpoise																
5 Seals																
6 Goosefish															0.01	
7 Coastal sharks	0.033		0.03				0.05								0.004	
8 Marine birds																
9 Striped bass																
10 Weakfish						0.01			0.02							
11 Snapper / grouper			0.01			0.01	0.069		0.05	0.026				0.01		
12 Baleen whales																
13 Jacks	0.072		0.02				0.01									
14 Spiny dogfish						0.005									0.01	
15 Benthic piscivores		0.01	0.018				0.01		0.005							
16 Black seabass						0.01									0.01	
17 Demersal piscivores			0.012	0.1	0.044	0.032	0.02	0.122	0.02		0.046				0.02	
18 Octopods							0.05				0.038				0.01	
19 Cods & hakes		0.05		0.01	0.185	0.02			0.01	0.01				0.01	0.01	
20 Redfish					0.004	0.02			0.01							
21 Lg. pel. planktivores	0.193		0.211		0.003	0.06					0.012		0.032		0.15	
22 Mackerel	0.22	0.03	0.167	0.04	0.014	0.09	0.026				0.048		0.054	0.142	0.218	0.276
23 Drum / croaker	0.001	0.01	0.001			0.02			0.05						0.01	
24 Benth. Invert. eaters			0.037			0.02	0.03		0.05		0.119				0.02	
25 Butterfishes		0.11								0.038					0.01	
26 Squid	0.106	0.195	0.12	0.1	0.148	0.18	0.11	0.263	0.05	0.09	0.004	0.1	0.019	0.099	0.05	0.05
27 Atlantic salmon	0.001		0.001	0.001	0.001		0.001									
28 Atlantic menhaden	0.061	0.015	0.055		0.243		0.029		0.055		0.088		0.195		0.01	
29 Forage fish	0.061	0.438	0.055	0.639	0.08	0.15	0.029	0.26	0.23	0.654	0.18	0.59	0.195	0.262	0.069	0.15
30 Dem. Planktivores						0.02			0.05		0.03				0.01	0.022
31 Tilefish																
32 Flounders		0.01	0.001		0.014	0.064	0.05		0.05					0.05	0.023	
33 Euphausiids									0.05			0.1		0.035	0.001	0.056
34 Scup						0.01										
35 Lobsters	0.001		0.001				0.05			0.01	0.019			0.011	0.02	0.05
36 Ocean pout		0.049				0.01			0.02					0.021	0.035	
37 Stomatopods											0.02		0.007			
38 Dem. Invert. eaters	0.111	0.01	0.129	0.1	0.193	0.032	0.186	0.122	0.07	0.026	0.174		0.413		0.02	
39 Rays & skates			0.01			0.079	0.15		0.02						0.02	
40 Jellies														0.163		
41 Mysids						0.01				0.038		0.1			0.01	
42 Macrozooplankton	0.019		0.02			0.139		0.205	0.04	0.016	0.045	0.05	0.005	0.055	0.06	
43 Crabs	0.031		0.031		0.004		0.05		0.05	0.021	0.1		0.005	0.023	0.04	0.1
44 Spot				0.01	0.004	0.009		0.007				0.01				0.004
45 Shrimp	0.023		0.023				0.048	0.005	0.05	0.021	0.02		0.039	0.023	0.04	0.1
46 Echonoderms							0.01				0.018					
47 Sessile epibenthos	0.001		0.001													0.022
48 Polychaetes					0.032											0.056
49 Small crustaceans	0.008		0.008		0.032		0.001	0.014	0.05	0.051	0.039		0.03			0.045
50 Bivalves	0.001						0.001							0.085		0.067
51 Microzooplankton	0.015		0.02					0.002				0.05	0.006			
52 Phytoplankton																
53 Macrophytes							0.02									
54 Microphytobenthos																
55 Detritus														0.01	0.11	
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 4 cont. Diet composition of components of the Mid-Atlantic Bight model.

Prey \ Predator	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
1 Billfishes																	
2 Bluefish																	
3 Tunas																	
4 Dolphins & porpoise																	
5 Seals																	
6 Goosefish																	
7 Coastal sharks																	
8 Marine birds																	
9 Striped bass																	
10 Weakfish																	
11 Snapper / grouper	0.014																
12 Baleen whales																	
13 Jacks	0.002																
14 Spiny dogfish																	
15 Benthic piscivores			0.005													0.001	
16 Black seabass																	
17 Demersal piscivores	0.009						0.026										
18 Octopods	0.011																
19 Cods & hakes			0.01													0.001	
20 Redfish	0.002		0.01														
21 Lg. pel. planktivores	0.008																
22 Mackerel	0.1		0.08													0.008	
23 Drum / croaker	0.002																
24 Benth. Invert. eaters	0.039	0.1					0.022	0.02									
25 Butterfishes			0.002													0.005	
26 Squid	0.003		0.02			0.04	0.002	0.02	0.04	0.02						0.02	
27 Atlantic salmon																	
28 Atlantic menhaden	0.097	0.025	0.05				0.069										
29 Forage fish	0.117	0.025	0.216			0.1	0.069	0.037					0.01		0.09	0.058	
30 Dem. Planktivores	0.008																
31 Tilefish																	
32 Flounders		0.1						0.001									
33 Euphausiids			0.119	0.46	0.1	0.11				0.136	0.1		0.15			0.017	
34 Scup																	
35 Lobsters	0.004	0.1	0.02	0.013		0.005		0.02					0.001			0.019	
36 Ocean pout								0.173									
37 Stomatopods	0.011	0.04					0.012	0.002									
38 Dem. Invert. eaters	0.257	0.2					0.134							0.02			
39 Rays & skates		0.05						0.013								0.003	
40 Jellies									0.197				0.014				
41 Mysids			0.005	0.1	0.05	0.048		0.006		0.05	0.1		0.033		0.1	0.045	0.05
42 Macrozooplankton	0.03		0.14	0.08	0.8	0.339	0.04	0.088	0.171	0.195	0.2	0.5	0.33	0.337		0.111	0.5
43 Crabs	0.05	0.1	0.02	0.021		0.01	0.068	0.03					0.001	0.023	0.05	0.02	
44 Spot															0.01		
45 Shrimp	0.07	0.1	0.02	0.026		0.01	0.153	0.03					0.001	0.086	0.05	0.02	
46 Echonoderms	0.007	0.03	0.001											0.004		0.056	
47 Sessile epibenthos		0.03					0.065		0.184					0.016	0.05	0.042	
48 Polychaetes			0.092			0.027		0.05	0.368	0.387	0.1		0.02		0.3	0.305	0.05
49 Small crustaceans	0.07		0.14	0.3		0.15	0.29	0.11	0.026	0.202	0.5		0.14	0.177	0.35	0.15	0.03
50 Bivalves		0.1	0.05			0.01		0.4		0.01						0.058	
51 Microzooplankton	0.086				0.05	0.151	0.027		0.013			0.5	0.15	0.337			0.27
52 Phytoplankton													0.1				0.05
53 Macrophytes	0.002						0.009										
54 Microphytobenthos																	
55 Detritus	0.001						0.014						0.05			0.06	0.05
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 4 cont. Diet composition of components of the Mid-Atlantic Bight model.

Prey \ Predator	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**
1 Billfishes																		
2 Bluefish																		
3 Tunas																		
4 Dolphins & porpoise																		
5 Seals																		
6 Goosefish																		
7 Coastal sharks																		
8 Marine birds																		
9 Striped bass																		
10 Weakfish																		
11 Snapper / grouper						0.011												
12 Baleen whales																		
13 Jacks																		
14 Spiny dogfish																		
15 Benthic piscivores																		
16 Black seabass																		
17 Demersal piscivores						0.006												
18 Octopods					0.002													
19 Cods & hakes						0.005												
20 Redfish																		
21 Lg. pel. planktivores																		
22 Mackerel																		
23 Drum / croaker																		
24 Benth. Invert. eaters		0.03			0.003													
25 Butterfishes																		
26 Squid	0.046			0.15	0.004	0.01												
27 Atlantic salmon																		
28 Atlantic menhaden		0.01			0.05													
29 Forage fish	0.04	0.01		0.04	0.03	0.08												
30 Dem. Planktivores																		
31 Tilefish																		
32 Flounders						0.016												
33 Euphausiids						0.054												
34 Scup																		
35 Lobsters	0.016		0.02			0.02												
36 Ocean pout						0.004												
37 Stomatopods																		
38 Dem. Invert. eaters		0.09		0.01	0.02	0.011												
39 Rays & skates		0.002																
40 Jellies																		
41 Mysids			0.03	0.02	0.02										0.01			
42 Macrozooplankton	0.035		0.1	0.05	0.151	0.045	0.23	0.12		0.11	0.08	0.12		0.045	0.005	0.005		
43 Crabs	0.033	0.17	0.03	0.07	0.005	0.02												
44 Spot	0.007																	
45 Shrimp	0.033		0.03	0.15	0.02	0.02				0.02	0.03							
46 Echonoderms		0.08	0.376	0.02	0.058								0.023					
47 Sessile epibenthos	0.046	0.07			0.065								0.102	0.01				
48 Polychaetes	0.5		0.131	0.02	0.017	0.092		0.02		0.07	0.06	0.03			0.02	0.03		
49 Small crustaceans	0.151	0.09	0.091	0.03	0.23	0.098		0.03		0.1	0.097	0.03	0.1	0.02	0.015	0.015	0.01	
50 Bivalves	0.093	0.334	0.122	0.11	0.065	0.22				0.22	0.142		0.009					
51 Microzooplankton					0.02		0.67	0.5	0.72	0.01		0.14		0.045	0.05	0.05		
52 Phytoplankton					0.008			0.3	0.28			0.09	0.028	0.235	0.1	0.05	0.25	1
53 Macrophytes		0.039	0.04	0.01	0.102					0.05	0.015		0.169			0.05		
54 Microphytobenthos		0.025	0.01	0.12	0.027			0.03		0.21		0.07	0.099	0.065	0.3	0.3	0.24	
55 Detritus		0.05	0.02	0.2	0.104	0.29	0.1			0.21	0.576	0.52	0.47	0.58	0.5	0.5	0.5	
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

disappear when biomass parameters for whole blocks of interacting species are unknown. Nevertheless, the uncertainties highlighted by the present model belie the ultimate strength of this exercise. Reconciled trophic models (e.g., balanced Ecopath models) are road maps of what is *not* known about an ecosystem.

In addition to this surprising paucity of biomass estimates in general, two specific examples of highlighted uncertainty are crabs and shrimps. These groups stood out as considerably unbalanced in the initial run of three recently constructed models of east coast U.S. ecosystems: the West Florida Shelf model (Mackinson *et al.*, 2000), the South Atlantic States shelf model (Okey and Pugliese, this volume), and the Middle Atlantic Bight shelf model (the present straw-man model). This indicates that the biomass of shrimps, and particularly crabs might be underestimated by group-specific assessments in these regions, or that these groups are overestimated in the specified diet compositions of fishes and other predators. Both of these alternatives are equally reasonable because only adult (and 'fishery sized') forms are normally assessed, whereas most of the biomass of crabs and shrimps might occur in juvenile or smaller forms, and because crustaceans are expected to linger in stomach contents of fishes and other predators while soft-bodied organisms are digested (and disappear) more quickly.

An alternative explanation is that the estimates of biomass or consumption rates of the predators of these crustaceans are overestimated. This shrimp and crab dilemma is discussed further in Okey and Nance (in Mackinson et al. 2000) and Mackinson and Okey (in Mackinson et al. 2000). Whatever the reasons for these discontinuities, the exercise of constructing Ecopath models can serve as an impetus for focusing detective work on weak (poorly known) junctures in a system.

The purpose of this 'straw-man' model of the Middle Atlantic Bight continental shelf was to provide a quantitative framework and a vehicle for the refinement of the model's input parameters so that a cohesive and useful view of the whole ecosystem can emerge. It would be prudent at this stage to focus on refinement and tuning rather than on shortcomings of the model's structure, especially since particular characteristics are taken from previous assessments and syntheses (Table 1). In its present form, and prior to simulation exercises, this model tells us little about the system that was not already known by experts. However, it provides an accessible view of the system and enables new explorations of system mechanisms and dynamics. It also allows development of sustainable strategies human interactions with this ecosystem.

The purpose of this iteration is for criticism that will lead to improvement. I recommend that experts in the various biotic components of the system be identified and assembled. Each of these experts could then scrutinize the component for which they have expertise (paying particular attention to biomass estimates) and they could develop new estimates based on updated information.

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Numerous individuals at the National Marine Fisheries Service, particularly at the Northeast Fisheries Science Centre, shared many years of information about the Middle Atlantic Bight system, especially some of the existing unpublished diet composition data. These data were provided in the spirit of sharing, and because they represent public information, but they were provided without official endorsement of my uses for them, or my interpretations. I am particularly thankful for the help of Jason Link, who provided excellent comments and advice, and carefully scrutinized an early draft. I am disappointed that the time constraints placed upon the delivery of this preliminary work prevented all of his concerns from being addressed. Thanks also go to Johanna Heymans, whose sharing of information enabled this 'straw-man' model to be constructed within the allotted time frame. Also, Sylvie Guénette should be congratulated for tolerating delays. The Pew Charitable Trusts of Philadelphia, USA initiated and supported the *Sea Around Us* project at the UBC Fisheries Centre, which funded the present work.

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