A PRELIMINARY ECOPATH MODEL OF THE ATLANTIC CONTINENTAL SHELF ADJACENT TO THE SOUTHEASTERN UNITED STATES

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ABSTRACT

The biological communities of the Atlantic continental shelf adjacent to the southeastern United States are well known, but this knowledge is not integrated into a cohesive description of that region. We constructed a preliminary food web model of this area using Ecopath with Ecosim, as a way to initiate a long-term process of integrating this knowledge, learning more about the structure and resiliency of the system, and helping to guide research priorities in the future. The current model is considered to be a first iteration that can be used as a vehicle to stimulate a more rigorous refinement effort in the near future. The ecologically defined area covered by this model extends from Cape Hatteras, North Carolina to the easternmost extent of the Florida Keys, and from the intertidal zone (or the entrance of estuarine systems) to the 500 m isobath. The time period characterized by this preliminary model is the four years from 1995 to 1998.

INTRODUCTION

Extensive estuaries, salt marshes, and barrier islands that protect sounds and waterways characterize the Atlantic coastline of the Southeastern United States. The gently sloping topography of this coastline gives away the subtidal bathymetry, which continues sloping smoothly to the east. The continental shelf is mostly covered with calcareous sands, but large ancient coral reef structures are exposed to varying degrees. These form hard-bottom reef areas that are locally referred to as "live bottoms" because of the diverse communities of algae, invertebrates, and fishes they support. The Gulf Stream flows from south to north along the coast transporting animals and plants and defining ecological interfaces. Meanders and intrusions of the Gulf Stream advect the underlying nutrient rich slope waters onto the shelf (Mallin *et al.* 2000).. This region as a whole supports a diverse assemblage of marine organisms, as it is somewhat of an ecological interface, or gradient, between warm-water and cold-water species assemblages. We refer the reader to Mallin *et al.* (2000) for a general description of the ecological setting, processes, and related research. A brief overview of special habitats is presented below.

Human activities along the east coast of the southeastern United States have influenced the adjacent continental shelf ecosystem for thousands of years, as native Americans conducted some limited artisanal fisheries and modified fire regimes and the vegetation in upland watersheds (e.g., Cronon, 1983). Modifications to the ecology of the continental shelf ecosystem accelerated soon after the arrival of Europeans, who began fishing coastal waters (e.g., Mowat, 1984; Reeves *et al.*, 1999) in addition to introducing domesticated livestock, weed plants, disease, and new kinds of agriculture (e.g., Crosby, 1986).

Other profound anthropogenic modifications to this continental shelf occurred during the 20th century with the widespread use of powered fishing and whaling vessels, and coastal urbanization and industrialization. One particularly destructive type of fishing is bottom trawling, which destroys biogenic seafloor habitat in addition to simply removing fishes (Watling and Norse, 1998; Turner *et al.*, 1999).

Trawling activity is intense in this area, and little doubt remains that these activities have considerably modified the continental shelf. The continental shelves of the southeastern United States as a whole are also very important for recreational fishing. Fisheries landings peaked around 1980 in this region, and have declined substantially since that time. According to Mallin *et al.* (2000), "overfishing has lead to serious declines in many wild fish stocks" in this area. The human population of this region is still growing rapidly, and pollution of various types (and associated algal blooms, etc.) also stands out as a serious and growing problem.

The U.S. 'South Atlantic Bight' continental shelf

The area of scrutiny for the preliminary Ecopath model we develop here extends from Cape Hatteras in North Carolina to the easternmost extent of the Florida Keys, and from the intertidal and the entrance of estuarine systems to the 500 m isobath. This coastal region and continental shelf constitutes a large bight, which is locally referred to as the "South Atlantic Bight," though it defines a portion of the western limit of the North Atlantic Ocean. The time period characterized by this preliminary model is four years during in the late 1990s (1995-1998). The area covered was estimated to be 174,300 km^2. The slope of the sea floor steepens seaward of the 200 m isobath (and sometimes shallower); for example, the area delineated by the 200 m isobath is estimated to be 133,300 km^2, which is only 24% less than the area delineated by the 500 m isobath.

'Essential fish habitat' in the South Atlantic Bight

The following summaries represent a snapshot of the important habitat types in the region that serve as 'Essential Fish Habitat' for federally managed species. The description and distribution of essential fish habitat includes estuarine inshore habitats, mainly focusing on North Carolina, South Carolina, Georgia, and the Florida east coast as well as adjacent offshore marine habitats (e.g., coral, coral reefs, and live/hard bottom habitat, artificial reefs, *Sargassum* habitat and the water column). The vast array of species using these habitats at different times and in different locations implies that these habitats are essential for the functioning of a healthy ecosystem in this region.

This is a brief review of the descriptions in the South Atlantic Fishery Management Council Habitat Plan (SAFMC, 1998a) and the Comprehensive Habitat Amendment (SAFMC, 1998b) developed for the purpose of designation and regulatory protection of Essential Fish Habitat. The emphasis here is on interrelationships between habitat and managed species and their prey, as well as endangered and threatened species. Such habitat considerations will ultimately prove crucial for the construction of refined Ecopath model iterations and for spatially explicit simulations after refinement.

Estuarine/Inshore Fish Habitat

Estuarine inshore habitats include estuarine emergent vegetation (salt marsh and brackish marsh), estuarine shrub/scrub (mangroves), seagrass, oyster reefs and shell banks, intertidal flats, palustrine emergent and forested (freshwater wetlands), and the estuarine water column.

Estuarine marshes form a complex ecosystem that is vital to wildlife including endangered and threatened species, furbearers and other mammals, waterfowl, wading birds, shore and other birds, reptiles and amphibians, shellfish, and invertebrates. In contrast to freshwater marshes, salt marshes have low species diversity of the higher vertebrates, but high species diversity of invertebrates, including shellfish, and fishes. Optimal estuarine habitat conditions for managed species' spawning, survival, and growth depends on the structural integrity and the environmental quality of these habitats. These marsh systems are very important nursery areas in North Carolina, South Carolina, Georgia, and Florida.

Mangrove habitat can be classified into six major types based on geological and hydrological process: riverine, overwash, fringe, basin, dwarf, and hammock, while mangrove-related fish communities can be organized along various environmental gradients including salinity, mangrove detritus dependence, and substrate.

Seagrass beds in North Carolina and Florida are preferred habitat areas for many managed species including white, brown, and pink shrimp, red drum, and estuarine dependent snapper and grouper species in the larval, juvenile and adult phases of their life cycle. Seagrass meadows provide substrates and environmental conditions that are essential for feeding, spawning, and growth of a number of managed species. Seagrass meadows are complex ecosystems that provide primary production, structural complexity, energy regime modification, shoreline stabilization, and nutrient cycling.

Oyster and shell habitat in the South Atlantic can be defined as the natural structures composed of oyster shell, live oysters, and associated organisms, aside from scattered oysters in marshes and mudflats and wave-formed shell windrows. Both intertidal and subtidal populations are found in the tidal creeks and estuaries of the South Atlantic. The ecological conditions encountered are diverse and the oyster community is not uniform throughout this range. Where the tidal range is large the oyster builds massive, discrete reefs in the intertidal zone. In wind-driven lagoonal systems, like Pamlico Sound in North Carolina, oyster assemblages consist mainly of subtidal beds. Oysters are found at varying distances up major drainage basins depending upon typography, salinity, substrate, and other variables. A whole suite of organisms is associated with oyster beds at various times of the year.

Tidal flats are critical structural components of coastal systems that serve as feeding grounds and refuges for a variety of animals. This dynamic habitat takes the form of (1) nursery grounds for early developmental stages of benthic oriented estuarine species; (2) refuges and feeding grounds for forage species of fishes; and (3) feeding grounds for specialized predators. Tidal flat habitat is extremely variable along the coast. North Carolina and Florida are largely micro-tidal (0-2m tidal range) with extensive barrier islands and relatively few inlets to extensive sound systems. In these areas wind energy has a strong affect on intertidal flats. The coasts of South Carolina and Georgia are meso-tidal (2-4m) with short barrier islands and numerous tidal inlets so that tidal currents are the primary force.

Palustrine emergent systems include tidal and non-tidal marshes. A large amount of the energy present in the palustrine emergent vegetation may be exported out of the system. Tidal currents, river currents, and wind energy all act to transport organic carbon downstream to the estuary, which is the nursery area for many managed species. Currents can also transport this material offshore. Migrating consumers, such as larval and juvenile fish and crustaceans, may feed within this dynamic palustrine habitat and then move on to the estuary or ocean. Thus, this organic carbon is also transported by trophic means.

Submersed rooted vascular vegetation in tidal fresh- or saltwater portions of estuaries and their tributaries performs the same functions as those described for seagrasses. Specifically, aquatic bed meadows possess the same four attributes: 1) primary productivity; 2) structural complexity; 3) modification of energy regimes and sediment stabilization; and 4) nutrient cycling.

The estuarine water column habitat is composed of horizontal and vertical components. Horizontally, salinity gradients (decreasing landward) strongly influence the distribution of biota, both directly (physiologically) and indirectly (e.g., emergent vegetation distribution). Horizontal gradients of nutrients, decreasing seaward, affect primarily the distribution of phytoplankton and, secondarily, organisms utilizing this primary productivity. Vertically, the water column may be stratified by salinity (fresh water runoff overlaying heavier salt water), oxygen content (lower values at the bottom associated with high biological oxygen demand due to inadequate vertical mixing), and nutrients, pesticides, industrial wastes, and pathogens (can build up near the bottom).

Marine/Offshore Fish Habitat

Marine offshore habitats include live/hard bottom, coral and coral reefs, artificial/manmade reefs, pelagic *Sargassum,* soft bottoms, and water column habitat.

Major fisheries habitats on the continental shelf along the southeastern United States from Cape Hatteras to Cape Canaveral can be organized into five general categories: coastal, open shelf, live/hard bottom, shelf edge, and lower shelf based on type of bottom and water temperature. Each of these habitats harbors a distinct association of demersal fishes and invertebrates. The description of this essential fish habitat in this entire region can be separated into two sections: (a) Cape Hatteras to Cape Canaveral; and (b) Cape Canaveral to the easternmost extent of the Florida Keys. These regions represent temperate, wide-shelf systems and tropical, narrow-shelf systems, respectively. The zoogeographic break between these regions typically occurs between Cape Canaveral and Jupiter Inlet.

‘Live bottom’ areas are important habitat for warm-temperate and tropical species of snappers, groupers, and associated fishes including 113 species of reef fish representing 43 families of predominately tropical and subtropical fishes off the coasts of North Carolina and South Carolina. These carbonate ‘live bottom’ outcroppings occur amidst a vast plain of sand and mud, often less than one meter thick. Live/hard bottom usually occurs in the zone between 15 and 35 fathoms, and at the shelf break. Steep cliffs and ledges characterize the shelf break, which occurs between approximately 35 to 100 fathoms.

Coral communities exist throughout the region from nearshore environments to continental slopes and canyons, including the intermediate shelf zones. Habitats supporting corals and coral-associated species can be categorized based on their physical and ecological characteristics. Corals might dominate a habitat, be a significant component, or be individuals within a community characterized by other fauna, depending on ecological conditions and history. The coral reefs of shallow warm waters support a wide array of hermatypic and ahermatypic corals, finfish, invertebrates, plants, and microorganisms. Hard bottoms and hard banks, found on a wider bathymetric and geographic scale, often possess high species diversity but may lack hermatypic corals, the supporting coralline structure, or some of the associated biota. In deeper waters, large elongate mounds called deepwater banks, hundreds of meters in length, often support a rich fauna compared to adjacent areas. Finally, solitary corals can be dispersed throughout other communities (e.g., sandy bottoms).

Artificial reefs occur where structures or materials have been placed intentionally to create, restore or improve long-term habitat for the eventual exploitation, conservation, or preservation of marine ecosystems. Artificial reef hard bottom habitats are formed when a primary hard substrate is available for the attachment and development of epibenthic assemblages. This substrate is colonized when marine algae and larvae of epibenthic animals successfully settle and thrive, and demersal reef-dwelling finfish recruit to the new hard bottom habitat. Juvenile and adult life stages of a variety of interacting species of fish use this habitat for protection from predators, orientation in the water column, as a feeding arena, or as a spawning site.

The pelagic brown algae *Sargassum natans* and *S. fluitans* float on the surface of the ocean and form a dynamic structural habitat within warm waters of the western North Atlantic. Most pelagic *Sargassum* circulates between 20° and 40° N latitude and 30° W longitude and the western edge of the Florida Current/Gulf Stream. The greatest concentrations are found within the North Atlantic Central Gyre in the Sargasso Sea, but large quantities frequently occur on the continental shelf off the southeastern United States. This material sometimes remains over the shelf for extended periods, entrained into the Gulf Stream, or cast ashore. During calm conditions, *Sargassum* forms large irregular mats or floats in small clumps. Langmuir circulation, internal waves, and convergence zones along fronts aggregate the algae along with other flotsam into long meandering rows termed 'windrows'. This habitat supports a diverse assemblage of marine organisms including fungi, micro-and macro-epiphytes, at least 145 species of invertebrates, over 100 species of fishes, four species of sea turtles, and numerous marine birds. The fishes associated with pelagic *Sargassum* in the western North Atlantic include juveniles and adults of a wide variety of species.

Specific water column habitats are defined in terms of gradients and discontinuities in temperature, salinity, density, nutrients, light, and other variables. These 'structural' components of the water column environment are not static, but change in both time and space. Characterization of any marine system should incorporate consideration of such water column habitat characteristics.

Many of the parameters of the model described in this paper are 'place holders' that were re-calculated using information recently gathered during an extensive literature survey for the construction of the West Florida Shelf model. A re-calculation of these parameters was conducted during the present effort based on the conditions and functional group aggregations that apply to the southeastern United States (Atlantic) continental shelf. A general goal of constructing an Ecopath model of this system is to provide a new whole-system analytical tool that would compliment existing tools in evaluating the effects of fishing on particular biological components, and the broader system. However, the analytical framework resulting from this effort is expected to have application to a host of issues relating to the effects of human activities on ecosystems, in addition to fishing.

The development of a preliminary Ecopath model for the South Atlantic Bight builds on the ecosystem approach taken by the South Atlantic Fishery Management Council to identify, describe and protect Essential Fish Habitat. This effort, when refined through a comprehensive workshop process, will provide further insight into the data limitations, interrelationships between and among species and their significant prey, and challenges that will be faced when developing a Fishery Ecosystem Plan for the region, which is being proposed for future amendments to the Magnuson-Stevens Fishery Conservation and Management Act in the United States.

METHODS

Polovina (1984) originally developed the Ecopath approach for application to the coral reefs of the French Frigate Shoals. Ecopath models are food web models that describe the state of biotic flows in an ecosystem. The most typical currency used is biomass wet-weight, and they include all biotic components of an ecosystem.

Ecopath models are static descriptions of flow, but the information in these static models can be used in the dynamic simulation routines Ecosim and Ecospace. Since its origin, 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 main reason for constructing Ecopath models. The immediate goal is to document the construction of an Ecopath model of the identified area.

Scores of applications of Ecopath with Ecosim can be found at: *www.ecopath.org*, along with the freely distributed software and documentation. Although the formulations and basic concepts of the Ecopath with Ecosim approach are presented in many accessible venues (including those cited above), the general approach is summarized below to provide a basic understanding of the model, the present simulation, and the results.

The Ecopath foundation

The parameters needed to construct an Ecopath model are represented in the Ecopath algorithm, which expresses the law of conservation of mass or energy (Equation 1). It says that the net production of a functional group equals (1) the total mass (or energy) of that group that is removed by predators and fisheries plus (2) the net biomass accumulation in the group plus (3) the net migration of the group's biomass plus (4) the mass flow to detritus. This equation balances a group's net production (terms to the left of the equal sign) with all sources of mortality or change for that group (terms to the right of the equal sign):

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

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 energy or biomass flows in food webs, and its implied thermodynamic constraints underscore the power of Ecopath models as a focal point for refinement of ecosystem information. The need to reconcile energy production and demand among food web components narrows the possible ranges of parameter estimates for particular groups, especially when good information exists for some, or many, groups in the system. Inclusion of a biomass accumulation factor and migration factor in the master equation of Ecopath distinguishes this modeling approach as an 'energy continuity' rather than a 'steady state' approach. Conservation of energy, or *continuity*, is assumed for every identified component of the ecosystem, and the system as a whole. This enables representation of changes in populations (i.e., functional groups), whether through migration or biomass accumulation (+/-).

The biological components of the ecosystem are represented using average values, or other meaningful measures of central tendency in populations. For example, biomasses, production rates, consumption rates, and diet compositions vary among seasons for many, if not most, species in aquatic and marine systems. Furthermore, these parameters change with size (~age), or ontogenetic stage, of the organisms in a system. The parameters used to characterize each group are averages that take into account both annual changes and ontogenetic changes. Experience with a variety of Ecopath models has shown that explicit inclusion of seasonal information does not change the basic answer provided by simulations, but rather makes the answer hard to interpret (C. Walters, UBC Fisheries Centre, pers. comm.). However, distinct ontogenetic changes within particular groups of interest can be represented by splitting a group into separate, but linked, ontogenetic pools, where one stage recruits into the other. Detailed age class structuring can now be incorporated in Ecopath models.

Assembling the list of species

Four main sources were used to assemble the list of over 600 species for the area covered here: summary data from the Southeast Area Monitoring and Assessment Program (SEAMAP) including a species list reviewed by SEAMAP personnel (P. Webster), the National Marine Fisheries Service (NMFS) commercial and recreational fish landings for North Carolina, South Carolina, Georgia, and the east coast of Florida (*www.st.nmfs.gov/st1/*); a species list recently developed for the West Florida Shelf system (Mackinson *et al.*, 2000); the NMFS marine mammal stock assessments; and two sea turtle the web sites; *www.nmfs.noaa.gov/prot_res/PR3/Turtles/turtles.html* and *www.cccturtle.org/species.htm*.

Aggregation of functional groups

A semi-systematic approach was taken to aggregate all species in the two continental shelf ecosystems into 42 functional groups. This was accomplished by organizing the list of species into groupings that were based on the functional roles of the species. Usually, this was operationally defined by diet compositions, but also by natural history characteristics. Special groups in the model included 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. Specialists were consulted to identify groups of special concern (e.g., baleen whales). The lists of species and aggregations of functional groupings were refined using the FishBase database (*www.fishbase.org*) and via a detailed review by SEAMAP personnel (P. Webster).

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), and the ratio of consumption to biomass (Q/B). Numerous sources were consulted during the assembly of basic parameter estimates, and these are listed in Appendix A. Other basic parameters include biomass accumulation, migration, the ratio of unassimilated to consumed food, and the ratio of production to consumption (P/Q).

The SEAMAP database is highlighted because these data represent the potential for estimating system-specific biomass estimates. These data consist of species-specific biomass measurements from trawl surveys that covered 129.57 km^2 trawled during the SEAMAP - SA program. For the purposes of this preliminary model, we assumed that the survey areas are representative of the South Atlantic States continental shelf as defined here. This is an problematic assumption, however, since SEAMAP resource surveys are restricted to shallow zones (*www.asmfc.org/Programs/Research/RESSVYS.HTM*). Extrapolation from these data should be made on a species-specific basis, and a reasonable approach to this end should be developed for future iterations of the model. We simply estimated the total biomass of each species captured during the SEAMAP monitoring program, divided by the total swept area, and summed the results according to the functional groupings determined in the model. Biomass estimates were calculated only for those groups that we thought would be reasonably represented by the SEAMAP sampling format. However, sampling efficiency of the gear was not accounted for when we estimated initial biomasses, and this undoubtedly lead to underestimations of biomasses in the sampled areas. The implications of these underestimations are discussed in the section on 'balancing the model.'

Most of the P/B and Q/B values in this preliminary model were derived through a process of re-aggregation of the data compiled for the West Florida Shelf model (Mackinson *et al.*, 2000) into the functional groups chosen for this model. These parameters were re-calculated based on this re-aggregation. This method will potentially bias the SAS model because these parameters were originally weighted based on relative abundances and relative consumption rates of the biological community of the West Florida Shelf. However, the literature search underlying the West Florida Shelf model was so extensive that confidence in the P/B and Q/B values in this neighboring model should be considered reasonably high, as long as differences in the relative abundances of species are taken into account (see Mackinson *et al.*, 2000). Since these two parameters (P/B and Q/B) tend to be biological properties that would be similar between physically similar systems, they are expected to be reasonable for application to the present model. Eventually, a more system-specific parameter estimation process can be undertaken.

Sources of diet composition information

The sources of diet composition information include an extensive literature review of fish diets by Mackinson *et al.* (2000) and a review of FishBase (Froese and Pauly, 2001). Randall's (1967) work was a primary source of fish diet information. Sources of diet information for all of the groups are listed in Appendix A. Representative diet compositions of functional groupings were estimated by consumption-weighted averages among species for which diet composition information could be identified. These estimates were made according to the functional group aggregation of the South Atlantic States continental shelf model. An electronic file of the diet composition matrix for this preliminary model is available from the first author.

Source of fisheries information

The commercial fisheries catch data from the NMFS database (*www.st.nmfs.gov/st1/commercial/index.html*) were re-compiled at the Fisheries Centre of the University of British Columbia in order to characterize the average annual commercial fisheries landings in North

Carolina, South Carolina, Georgia, and the east coast of Florida during the late 1990s (1995-1998). Recreational catches are probably significant in this system, but they were left out of this preliminary model. These data are available on the web at *www.st.nmfs.gov/st1/ recreational/index.html* and they should be included in future iterations. Discards were then taken to be 20% of the catch rates across-the-board, and these 'place-holder' discard values were then entered in the software's discard interface. Estimates of discards should be made for every fishery in operation in this region, and these should be entered into the next iteration of the model regardless of the reliability of these estimates. Assessment of discards can follow the example of FAO (1995) and STOA (1998).

Balancing the model

The South Atlantic States shelf model has undergone two preliminary iterations. The first involved shaping the structure of the model (e.g., the functional groupings) and assembling input parameters from the general literature and from models of nearby and related systems. The second iteration incorporated site-specific biomass estimations from the SEAMAP—SA program (SEAMAP-SA / SCMRD, 2000). Sixteen out of 42 groups were thermodynamically unbalanced the first time the 'basic parameters' were estimated. The ecotrophic efficiency of these unbalanced groups ranged from 1.09 to 27.07. The mean was 5.89 ± 1.54 SE. These unbalanced groups were all fish groups, except for squid, marine birds, and turtles. After SEAMAP biomass estimates were incorporated, 11 of the 42 groups were thermodynamically unbalanced, and the ecotrophic efficiency of these newly unbalanced groups ranged from 2.5 to 1,438.1, and the mean was 165.9 ± 127.8 SE. The new unbalanced groups included flounders, snappers, groupers, demersal invertebrate eaters, demersal piscivores, demersal omnivores, benthic piscivores, benthic invertebrate eaters, shrimps, crabs, stomatopods, and octopods. This considerably higher imbalance with the introduction of site-specific information might partially reflect low sampling efficiency of the SEAMAP trawls for some species, or an overestimation of some of the predator biomasses, consumption rates, or diets. A combination of these two general classes of error is the most probable explanation.

The first step during the initial balancing process was to minimize cannibalism within groups, as recommended by the Ecopath architects. In essence, minimizing cannibalism minimizes energy (mass) trapping, making available more energy for other components of the food web. The second step was to increase the entered ecotrophic efficiency (EE) values to provide more energy (mass) for consumers in the system. Most values were changed from 0.95 to 0.98, meaning that 98% of the net production of the corresponding group is consumed in the system.

The third step was to examine the consumption rates upon each unbalanced group, beginning with the most unbalanced group (in this case 'forage fish'). In cases where the higher rates of consumption were not supported by reliable diet compositions, the diets of predators were appropriately adjusted to decrease these consumption values. This meant that consumption on one group was shifted to another group where this made ecological sense. For example, it was observed that the EE value for tuna was low, and this presented the opportunity of shifting consumption from similar prey to tuna (which had been unrealistically under-exploited in our model). This is an ecologically reasonable adjustment since the full suite of ontogenetic stages of tuna is not explicitly represented in the model. It would be reasonable to assume that predators would switch from jacks, mackerel, and billfishes to tuna if the latter were more available. A related approach is to reduce the consumption rate of predators having a proportionally high impact on unbalanced groups. The Q/B value was accordingly reduced approximately 10% for the following groups: mackerel, snapper, grouper, demersal piscivores, toothed cetaceans, tuna, and pelagic piscivores.

Adjustment of biomass estimates was used liberally during the initial balancing procedure because the initial biomass estimates were considered to be placeholders, as many of them were modified from a recently constructed model of the West Florida Shelf (Mackinson *et al.*, 2000). This resulted in a balanced model with all the components (functional groups) of the South Atlantic States, but with limited connection to data from the South Atlantic States continental shelf. The next step was to incorporate biomass estimates from SEAMAP trawl data.

Table 1 shows the degree of adjustment to the SEAMAP biomass estimates made by the Ecopath software in order to obtain thermodynamic consistency with the other input parameters in the present model. Ecopath increased the biomass estimates in all but two cases. If confidence in the input data throughout the model were high, the inverse of the adjustment factor could be considered an estimate of the sampling efficiency of the SEAMAP trawls for each of the species presented.

Table 1. Degree of adjustment to rudimentary biomass estimations based on SEAMAP-SA / SCMRD (2000) using the preliminary Ecopath model of the South Atlantic States shelf. The inverse of these adjustments can be considered trawl sampling efficiency estimates, or a roadmap for future refinement of this preliminary model.

Functional group	SEAMAP estimate ($t \cdot km^{-2}$)	Ecopath estimate ($t \cdot km^{-2}$)	Adjustment factor
Sharks (and alligators)	0.104	0.104	1
Flounder	0.018	0.346	19
Drum and croaker	0.722	0.722	1
Snappers	0.001	0.125	125
Groupers	0.001	0.125	125
Benthic rays/skates	0.465	0.465	1
Demersal invertebrate-eaters	0.126	2.416	19
Demersal piscivores	0.028	0.203	7
Demersal omnivores	0.111	0.890	8
Benthic piscivores	0.038	0.140	4
Benthic invertebrate-eaters	0.014	0.602	43
Shrimps	0.030	7.639	255
Crabs	0.022	9.261	421
Stomatopods	0.002	2.845	1423

However, in the case of this model iteration, the biomass estimates calculated by Ecopath might be considered by some to be unreasonably large. This provocative result should be considered as a roadmap for future refinement of model inputs (better input data tends to lead to a higher degree of internal consistency). Nevertheless, it is also reasonable that the biomass of shrimps, crabs, and stomatopods are typically underestimated in assessments, as indicated by other east coast Ecopath models (e.g., Mackinson *et al.*, 2000). Indeed, assessments focus on adult forms and fishery sizes, but the bulk of the biomass of a species or functional group can occur at smaller sizes or life stages. Alternatively, these groups might be relatively overemphasized in the gut contents of their predators because their chitonous integuments persist longer, relative to soft-bodied prey.

RESULTS

The number of trophic connections in this marine ecosystem renders food web diagrams somewhat incomprehensible. Table 2 shows some of the basic parameters of the South Atlantic States continental shelf model. Summary statistics for the system are presented in Table 3. The diet composition matrix is not presented, but is available from the first author.

Table 3. Basic summary statistics for the preliminary Ecopath model of the South Atlantic States continental shelf. Values are expressed in wet weight.

Parameter	Value	Units
Sum of all consumption	6089.381	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all exports	1807.018	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all respiratory flows	2529.107	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all flows into detritus	4092.102	$t \cdot km^{-2} \cdot year^{-1}$
Total system throughput	14518.000	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all production	5420.000	$t \cdot km^{-2} \cdot year^{-1}$
Calculated total net primary production	4335.955	$t \cdot km^{-2} \cdot year^{-1}$
Net system production	1806.848	$t \cdot km^{-2} \cdot year^{-1}$
Total biomass (excluding detritus)	469.737	$t \cdot km^{-2}$
Total catches	0.787	$t \cdot km^{-2} \cdot year^{-1}$
Mean trophic level of the catch	3.01	-
Gross efficiency (catch/net p.p.)	0.000181	-
Total primary production/total respiration	1.714	-
Total primary production/total biomass	9.231	-
Total biomass/total throughput	0.032	-
Connectance Index	0.281	-
System omnivory Index	0.217	-

Table 2. Basic parameters of the preliminary Ecopath model of the South Atlantic States continental shelf. Values in bold have been calculated with the Ecopath software; other values are empirically based inputs. Omnivory index (= variance of prey trophic levels) is denoted by 'OI'.

Group	**Trophic level**	**OI**	**Biomass (t·km^{-2})**	**P/B (year^{-1})**	**Q/B (year^{-1})**	**EE**
Billfishes	**4.3**	**0.371**	0.005	0.44	5.29	**0.962**
Sharks (& alligators)	**4.3**	**0.302**	0.104	0.43	4.18	**0.628**
Tuna	**4.2**	**0.316**	0.024	0.85	12.00	**0.801**
Toothed cetaceans	**4.1**	**0.174**	0.058	0.10	27.00	**0.000**
Mackerel	**4.0**	**0.069**	0.207	0.38	8.00	**0.941**
Groupers	**4.0**	**0.202**	**0.125**	0.70	5.00	0.950
Jacks	**3.9**	**0.111**	0.068	0.56	9.20	**0.854**
Snappers	**3.9**	**0.225**	**0.125**	0.57	5.40	0.950
Pelagic piscivores	**3.9**	**0.270**	0.232	0.86	13.50	**0.837**
Octopods	**3.9**	**0.193**	**0.072**	3.10	7.30	0.980
Demersal piscivores	**3.8**	**0.193**	**0.203**	0.84	8.10	0.950
Marine birds	**3.8**	**0.716**	0.001	0.10	80.00	**0.800**
Benthic piscivores	**3.8**	**0.340**	**0.140**	0.39	8.73	0.950
Drum and croaker	**3.4**	**0.254**	0.722	0.47	7.34	**0.915**
Benthic invert-eaters	**3.4**	**0.164**	**0.602**	1.73	13.57	0.950
Squid	**3.4**	**0.205**	1.900	2.43	33.00	**0.966**
Flounder	**3.3**	**0.148**	**0.346**	0.30	9.46	0.950
Benthic rays/skates	**3.3**	**0.452**	0.465	0.40	8.96	**0.769**
Lobsters	**3.2**	**0.325**	**0.364**	0.90	8.20	0.950
Baleen whales	**3.2**	**0.213**	0.144	0.05	10.90	**0.000**
Demers. planktivores	**3.1**	**0.060**	**0.114**	2.60	10.00	0.980
Sea turtles	**3.1**	**0.412**	0.007	0.19	3.50	**0.471**
Dem. invert-eaters	**3.1**	**0.472**	**2.416**	0.77	8.71	0.950
Stomatopods	**3.0**	**0.653**	**2.845**	1.34	7.43	0.980
Pelagic planktivores	**3.0**	**0.304**	**9.416**	0.89	8.54	0.980
Other fishes	**3.0**	**0.086**	**22.240**	0.70	7.04	0.980
Forage fishes	**2.9**	**0.202**	**25.065**	0.93	13.88	0.990
Jellies	**2.8**	**0.160**	**0.270**	40.00	80.00	0.950
Crabs	**2.7**	**0.316**	**9.261**	1.38	8.50	0.980
Shrimp	**2.7**	**0.268**	**7.639**	3.16	19.20	0.980
Demers. omnivores	**2.6**	**0.382**	**0.890**	1.47	21.87	0.950
Echinoderms	**2.3**	**0.225**	25.000	1.20	3.70	**0.709**
Sessile epibenthos	**2.2**	**0.144**	**78.605**	0.80	9.00	0.850
Benthic macro & meio	**2.0**	**0.040**	**67.314**	5.08	21.52	0.990
Bivalves	**2.0**	**0.011**	55.000	1.22	23.00	**0.813**
Manatees	**2.0**	**0.000**	0.001	0.10	36.50	**0.000**
Zooplankton	**2.0**	**0.000**	36.500	13.00	43.30	**0.910**
Macroalgae	**1.0**	**0.000**	**52.096**	4.00	-	0.800
Microphytobenthos	**1.0**	**0.000**	37.000	55.57	-	**0.328**
Phytoplankton	**1.0**	**0.000**	**5.645**	332.67	-	0.990
Sea grasses	**1.0**	**0.000**	**26.507**	7.30	-	0.500
Detritus	**1.0**	**0.362**	518.000	-	-	**0.559**

DISCUSSION

This preliminary model of the South Atlantic States continental shelf was constructed to provide a quantitative framework for the refinement of the model's input parameters so that a cohesive view of the whole marine ecosystem can emerge, and so that system-wide questions about the workings of the system can be explored. We suggest this model can be a focal point for scrutiny and criticism of input parameters, and thus act as a vehicle for a new view of the system to emerge. We recommend that experts in the various biotic components of the system be identified and involved into a coordinated and collaborative refinement strategy that would address suggestions and 'refinement negotiations' in a transparent and efficient manner.

Notwithstanding the natural limitations of broad-system modeling approaches, this model has tremendous potential to provide an accessible and useful view of the whole ecosystem for scientists, students, and the general public. This approach can become a critical complement to other available assessment and management tools currently in use or being developed, and can help bring us into the new era of ecosystem-based management. The dynamic simulation approaches that accompany the Ecopath with Ecosim approach are not addressed in the current paper, but descriptions of these are provided by Christensen and Pauly (1992), Walters *et al.* (1997), Walters *et al.* (1999), Christensen *et al.* (2000), Pauly *et al.* (2000), and Walters *et al.* (2000).

A process of refining the model by a working group of experts needs to be coordinated such that a central copy is maintained. Also this process should include several iterations of review and refinement. However, a practical sunset for the process should be clearly identified in order to apply the model to questions of interest in the system with a standard iteration of the model that is considered adequately useful.

Improvements to the model should begin with the broadest issues, such as issues of system definition and aggregation of functional groupings (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. That is to say, a particular sub-system of the model can be 'broken out' if the questions of interest relate to the articulation of that sub system. Suggested improvements should then proceed to the refinement and tuning of specific parameter estimates based on the research and scrutiny of experts.

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Appendix A. Sources of basic parameter estimates. The values used as inputs in the preliminary South Atlantic States continental shelf model were derived from these sources based on their application to the defined system, rather than being simply extracted.

Group	**Biomass (t·km^{-2})**	**P/B (year^{-1})**	**Q/B (year^{-1})**	**Diet composition**
Billfishes	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Sharks (& gators)	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Tuna	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Toothed cetaceans	NMFS (2000), Trites & Pauly (1998)	Matkin & Hobbs (1999b)	Kastelein *et al.* (1997) in Matkin & Hobbs (1999)	Vasconcellos (2000a)
Mackerel	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Groupers	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Jacks	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)	Randall (1967)
Snappers	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Pelagic piscivores	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Octopods	SEAMAP-SA / SCMRD (2000)	Buchan & Smale (1981) in Opitz (1993)	Guerra (1979)	Whitaker *et al.* (1991) in Grubert *et al.* (1999)
Demersal piscivores	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Marine birds	Vidal-Hernandez & Nesbitt (2000)	Acosta *et al.* (1998)	Vidal-Hernandez & Nesbitt (2000); Nilsson & Nilsson (1976)	Vidal-Hernandez & Nesbitt (2000)
Benthic piscivores	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Drum & croaker	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Benth invert-eaters	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Squid	Mendoza (1993)	Mendosa (1993) & Pauly *et al.* (1993)	Mendoza (1993)	Amaratunga (1983) in Mendoza (1993); Karpov & Cailliet (1978)
Flounder	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Topp & Hoff (1972)
Benthic rays/skates	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Lobsters	O'hop *et al.*, (unpublished data[a])	Arreguín-Sánchez *et al.* (1993)	Arreguín-Sánchez *et al.* (1993)	Martinez (2000)
Baleen whales	Dolphin (1987), NMFS (2000)	Matkin & Hobbs (1999a)	Dolphin (1987)	Okey (estimation)
Demers. planktivores		Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Sea turtles	Vasconcellos (2000 b)	Vasconcellos (2000b)	Polovina (1984)	Vasconcellos (2000b)
Dem. invert-eaters	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Stomatopods	SEAMAP-SA / SCMRD (2000)	Meyer & Caldwell (2000)	Meyer & Caldwell (2000)	Meyer & Caldwell (2000)
Pelagic planktivores	-	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Other fishes	-	-	-	Mackinson (2000)
Forage fishes	-	Mackinson (2000)	-	Mackinson (2000)

Appendix A. cont.

Group	Biomass ($t \cdot km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	Diet composition
Jellies		Okey *et al.* (1999), Graham (2000)	Purcell (1983), Graham (2000)	Graham & Kroutil (submitted); Okey *et al.* (1999)
Crabs	SEAMAP-SA / SCMRD (2000)	Ehrhardt & Restrepo (1989) in Okey & Meyer (2000)	Arreguín-Sánchez *et al.* (1993)	Okey & Meyer (2000)
Shrimp	SEAMAP-SA / SCMRD (2000)	Parrack (1981); Arreguín-Sánchez *et al.* (1993); Okey & Nance (2000)	Arreguín-Sánchez *et al.* (1993)	Huff &Cobb (1979 in Okey & Nance, 2000)
Demers. omnivores	SEAMAP-SA / SCMRD (2000)	Mackinson (2000)	Mackinson (2000)	Mackinson (2000)
Echinoderms	Okey (2000b)	Lewis (1981); Schwinghamer *et al.* (1986) in Opitz (1993)	Pauly *et al.* (1993)	Okey (2000a)
Sessile epibenthos	-	Odum & Odum (1955) & Sorokin (1987) in Opitz (1993)	Based on Wilkinson (1987) & Sorokin (1987) in Opitz (1993)	Okey (2000d)
Benth. macro & meio	-	Arreguín-Sánchez *et al.* (1993)	Arreguín-Sánchez *et al.* (1993)	Okey (2000c,e)
Bivalves	Arnold *et al.* (2000)	Arnold *et al.* (2000)	Guénette (1996)	Arnold *et al.* (2000)
Manatees	Vasconcellos (2000c), Rathbun *et al.* (1995), USFWS (1993)	B. Ackerman, pers. comm (in Vasconcellos, 2000c)	B. Ackerman, pers. comm. (in Vasconcellos, 2000c)	Bengtson (1981) & O'Shea (1986) from USFWS (1993)
Zooplankton	Sutton & Burghart (2000)	Sutton & Burghart (2000)	Sutton & Burghart (2000)	T.A. Okey (estimation)
Macroalgae	-	Luning (1990)	n/a	n/a
Microphytobenthos	Cahoon *et al.* (1990), Cahoon & Cooke (1992)	Cahoon & Cooke (1992)	n/a	n/a
Phytoplankton	-	Cahoon & Cooke (1992)	n/a	n/a
Sea grasses	-	P. Carlson, pers. comm.[b]	n/a	n/a
Detritus	Okey (2000b)	n/a	n/a	n/a

[a] Based on J. O'hop, M. Tupper, and S. Brown, Florida Marine Research Institute (unpublished data).

[b] P. Carlson, Florida Marine Resources Institute, personal communication, 3 March 2000.

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