An Overview of EMAX: The Northeast U.S. Continental Shelf Ecological Network

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Abstract

Notable changes have occurred in the Northeast U.S. Continental Shelf LME. To evaluate the response of this ecosystem to numerous human-induced perturbations, as well as to explore possible future scenarios, the Northeast Fisheries Science Center instituted the Energy Modeling and Analysis eXercise (EMAX). The primary goal of EMAX was to establish an ecological network model (i.e., a more nuanced energy budget) of the entire Northeast U.S. food web. The EMAX work focused on four subregions of the ecosystem from contemporary times (1996-2000), had 36 network “nodes” or biomass state variables across a broad range of the biological hierarchy, was highly interdisciplinary, and incorporated a wide range of key rate processes. The emphasis of EMAX was to explore the particular role of small pelagic fishes in the ecosystem. Various model configurations were constructed and psuedo-dynamic scenarios were evaluated to explore how potential changes to the small pelagic fishes can affect the rest of the food web. Our results show that small pelagic fishes are clearly keystone species in the ecosystem. There are some differences across the four EMAX regions reflective of the local biology, but major patterns of network properties are similar over space. Finally, EMAX will continue to play a critical role for the further development of EAF as: a catalogue of information and data; identifying major fluxes among biotic components of the ecosystem; a basis for further analytical models; a way to evaluate biomass tradeoffs; and a backdrop for a suite of other relevant, management and research questions.
Introduction

There have been numerous recent calls to adopt an ecosystem approach to fisheries (EAF or Ecosystem-based fisheries management, EBFM; here EAF and EBFM are used synonymously; e.g., Garcia et al., 2003, Garcia 2005, Link 2002). There many rationales for why EAF is an emerging approach. Central to these considerations are taking a more holistic look at an ecosystem and simultaneously evaluating tradeoffs among component biomass or user sectors (e.g., Larkin 1996, Link 2002, etc.).

One approach to explore holistic ecosystem perspectives and to examine biomass tradeoffs is to use ecosystem models. Within the wide variety of possible models one could use (Hollowed et al. 2000, Whipple et al. 2000), energy budgets and network analyses provide useful tools to evaluate relative biomass, system properties, and fluxes within an ecosystem. Many of these models allow one to explore the fate and flux of production within a system by explicitly tracking how the energy flows from various components of the system to one another. Of the many possible network models, we chose to use EcoPath (Christensen and Pauly 1992, Walters et al. 1997) and EcoNetwrk (Ulanowicz 2004, Ulanowicz and Kay 1991) as two models to allow us to evaluate various spatial, temporal, and hypothetical scenarios in our ecosystem of interest.

The Northeast United States continental shelf large marine ecosystem (hereafter, NEUS; Sherman 1991) is a highly productive ecosystem that has supported significant commercial fisheries for multiple centuries. The recent history of the component fish stocks has exhibited the classic cycles of excessive effort, stock declines, and iterations thereof until the point of sequential stock depletion (Fogarty and Murawski 1998, Murawski et al. 1997, Serchuk et al. 1994). Within NEUS, there are four main sub-
regions (Figure 1) that have different ambient fauna and thus slightly different fishing histories and environmental considerations. In this context, the major fishery-related events in the NEUS over the past several decades can be characterized loosely as the following sequence: an increase in small pelagic catches by foreign fleets, a continued increase in demersal groundfish catches, a precipitous decline in small pelagic stocks, a decline of some groundfish stocks, an effective cessation of the small pelagic fisheries (and expulsion of foreign fleets), a continual series of overfishing on an ever-increasing array of groundfish, an increase in elasmobranch stocks, the beginnings of an increase in small pelagic stocks, an establishment of elasmobranch fisheries, an increase in benthic invertebrate fisheries and stocks, the persistence of groundfish stocks at moderate to low levels, the persistence of groundfish fisheries at suboptimal yields, the decline of elasmobranch stocks and subsequently their fisheries, and the effective explosion of small pelagic stocks to what are now record highs (Serchuk et al. 1994, Murawski and Fogarty 1998, Link and Brodziak 2002, Overholtz 2002). While the various fisheries and their effects were occurring, notable changes to protected, endangered and threatened species (PETS; e.g. many marine mammals) have occurred, with many in more critical condition than 50 years ago (Waring et al. 2004). Additionally, shifts in non-targeted fauna (NEPA species; e.g. some benthos, some non-targeted fishes) also occurred (Link and Brodziak 2002), with some actually persisting at relatively stable levels or even increasing (Link and Brodziak 2002, Link 2005).

Overall, the general observation is that the ecosystem has undergone a shift from a vertical to a horizontal system (Link 1999) due to the resurgence of herring and mackerel. With this resurgence of herring and mackerel stocks, the question begs: how
important have these small pelagics become to the success of other commercial fish stocks, PETS, NEPA species, and ultimately the overall functioning of the ecosystem. This issue has become increasingly important as multiple stakeholders have begun exploring potential tradeoffs in the NEUS ecosystem.

Our objectives in this work were fourfold. First, we wanted to balance a contemporary energy budget of NEUS. Second, we wanted to construct an energy budget/network for each of the four sub-regions of NEUS. Third, we wanted to compare key network properties spatially across these four regions. Finally, we wanted to evaluate the relative importance of the small pelagics in this ecosystem. To achieve these and related objectives, the Northeast Fisheries Science Center (NEFSC) instituted the Energy Modeling and Analysis eXercise (EMAX). In some respects this document serves as an initial but partial report of that exercise.

Materials and Methods

Nodes & Data Sources

After a long series of iterations, we settled on 36 major nodes for the EMAX network (Figure 2). These represent the full range of the biological hierarchy, with organisms spanning < 10 µm to > 30 m. Most network nodes represent a broad range of functionally similar taxa, but also integrate across a wide range of diversity and ecological functionality. The species in each node can be found in a more detailed set of documentation (EMAX 2005). We particularly chose to include elements of the microbial loop (Azam et al. 1983) to help in the balancing, to better reflect reality, and to acknowledge some of the fundamental shifts in views of how the oceans function. Again,
our emphasis was on small pelagics so some of the nodes that may not greatly interact with those species were not necessarily grouped as they might have been with a different focus.

We limited our data usage, parameter estimation, and temporal coverage to the 1996-2000 time period. We did so for several reasons, chief of which was data availability, commonality of units, and spatio-temporal overlap for as many of the nodes as possible. We used an appropriate level of seasonality for each node integrated into an annual average for each estimate during this period. The units we chose to use were g wet weight m⁻².

There were five main elements critical to the construction of each node for the four NEUS networks. We estimated biomass, production, consumption, respiration, and diet composition for all nodes. Additionally, for some nodes it was germane to estimate other sources of removals- namely fisheries. Various approaches were used for all the nodes, ranging from literature bounding of values for some of the globally under-determined groups (e.g. bacteria, microzooplankton) to probabilistic estimates from multiple sampling regimes (e.g. some of the fishes). Further details of our estimation protocols and methods, for biomass, the various rates, and diet compositions, can be found in EMAX (2005).

We noted a qualitative pedigree of data “certainty” for each parameter of each node. An important distinction of our approach relative to many other energy budget and network modeling exercises is that we started the balancing protocol with all parameters having an initial estimate and did not use the models to estimate any parameter values. Certainly the models modified these values in the balancing protocols, but the point is
that, factually speaking without any hubris, we started with a degree of completeness where most other studies end up.

Models

We explored a broad myriad of energy budget and network models (and their associated software packages). After several iterations, we settled on using two models as our primary tools: EcoPath (Christensen and Pauly 1992, Walters et al. 1997) and EcoNetwrk (Ulanowicz 2004, Ulanowicz and Kay 1991). The pros and cons of each have been variously noted elsewhere (e.g., Allesina and Bondavalli 2003, Heymans and Baird 2000, Hollowed et al. 2000, Kavanagh et al. 2004, Ulanowicz 2004, Walters et al. 1997, Whipple et al. 2000). One reason we chose these two is the subtle differences in underlying philosophy and numerical solving approaches between the two programs (Heymans and Baird 2000). Other models we evaluated are also potentially very useful but were either redundant with the two we chose, focused on more qualitative network properties, were less user friendly, or obfuscated their underlying model structure. As such we did use them in this exercise.

The general balancing protocol we used was to take an input matrix (described above), walk through it with several diagnostics, re-examine all parameter values in workshops with a group of experts, and then use this as the initial model. In EcoPath, we then rebalanced the baseline input using EE as the primary constraint, attempting to get as many nodes as possible to <1. In EcoNetwrk we then rebalanced using the R/C ratio as the primary constraint, attempting to get as many nodes as possible ~>20%. Again, further details can be found in EMAX (2005).
Scenarios

Once a balanced, baseline model was obtained, various changes (Table 1) were subjected to the network which was then rebalanced. Although we have preliminary balanced networks for all four subregions, we chose to evaluate the various scenarios for only one of them, the Gulf of Maine. We executed the scenario rebalancing as a pseudo-dynamic modeling process, ultimately to see where the perturbed system would redistribute biomass and production after the changes were imposed. We executed all scenarios in both model packages.

For comparisons across regions and across scenarios, we examined a common set of network, cybernetic, and ecological statistics that are helpful components of these two software packages. Yet we primarily evaluated a set of biomass ratios and similar indicators (Link 2005) to particularly highlight the role of small pelagics.

Preliminary Results

General system observations

Overall, the biomass in this ecosystem was dominated by lower trophic levels. The system and its various sub-regions appear to be driven by bottom up processes (Figure 3b, 5a, 6). Most of these lower trophic level fluxes appeared to be concentrated in the pelagia rather than the benthos (Figure 3b, 4b, 5).

In all of our balancing exercises, using both software packages, the groups which were routinely modified and had the most impact on network balance were: bacteria, microzooplankton, gelatinous zooplankton, macrobenthos-other, and shrimp.
Interestingly, these groups were at the first two to three trophic levels. Two of these network nodes, bacteria and microzooplankton, were not originally part of our network but were included to allow us to better track detrital dynamics. Gelatinous zooplankton are notoriously difficult to estimate, and although all of our balancing exercises regularly lowered the standing stock biomass of this node, this node has the potential to strongly drive ecosystem dynamics.

When initially balancing an energy budget and then when rebalancing for the various scenarios, most of the changes were observed in consumptive flux rates and not in the biomass, with the few exceptions noted above (e.g. gelatinous zooplankton). What this implies is that the system is highly connected with a broad range of alternate energy pathways to and from any particular node.

In the entire network, we ended up with a network constructed of 36 nodes (Figure 2). Not all nodes are germane to each sub-region. Additionally, when balancing the models, we treated the two major fishery nodes as an external source of removals but not as a node directly. We also dealt with dissolved organic carbon by proxy using particulate organic detritus. Thus, as an example the Gulf of Maine region had 31 nodes. Calculating simple food web macrodescriptors (Link 1999), there were a possible of 480 species interactions (including the diagonal, i.e. cannibalism). Within this network, there were 361 observed interactions. Thus, the connectance of this network was on the order of 66%, a value that is high for most food webs. Although there are a plethora of other system indicators and cybernetic metrics that are extant and that we could examine in greater detail, we do not present them.
With few exceptions, both EcoPath and EcoNetwrk generally produced similar results (Figure 7 vs. 8, 9 vs. 10, 11 vs. 12). Although there were some differences when the finer details were examined, most model outputs were qualitatively similar. Additionally, in most instances the changes in the various scenarios were on the same order of magnitude. This was intriguing as the balancing routines and protocols for both software packages were slightly different.

Regional Comparisons

There are some differences across the four EMAX regions reflective of the local biology, but major the major patterns of network properties are surprisingly similar over space. Overall, in terms of biomass small pelagics were not the dominant fish nodes, rather the demersals were (Figure 3a, 4a). The upper trophic level nodes were less than 20%, often less than 2%, of the small pelagic biomass (Figure 3a). It was apparent that the further south one goes, the less prominent marine mammals became (Figure 3a). Conversely, small pelagics comprised a larger proportion of fish biomass in the Gulf of Maine than in other regions (Figure 3a, 4a). Interestingly, there were relatively less small pelagics on Georges Bank than in other regions. Also, Southern New England appeared to be an important area for larval and juvenile fish, even more so than Georges Bank.

As a fraction of lower trophic levels, biomass of small pelagics was generally quite small (Figure 3b). However, there were three times and one and a half times as much small pelagic biomass compared to zooplankton on Georges Bank and in the Mid-Atlantic Bight, respectively (Figure 3b). But when one considers micronekton and
shrimp, other key prey of small pelagics, these ratios were mitigated to much lower numbers in all regions.

As would be expected, there was more standing stock biomass in the benthos than the zooplankton, especially in Southern New England (Figure 3b). Macrobenthos nodes in particular were the dominant invertebrate in terms of standing stock biomass (Figure 4b), especially so in the Mid-Atlantic Bight. Interestingly, gelatinous zooplankton comprised 20-30% of all invertebrate biomass in this ecosystem. Conversely, most benthos were much less productive than zooplankton (Figure 5a). Both broad groups at the second trophic level (benthos, zooplankton) were about one-tenth to one-fifth as productive as primary producers (Figure 5a), with zooplankton much more productive than the benthos by a factor of 4 to 10. These ratios did not include any estimates of recycling or bacterial production. The Mid-Atlantic Bight had the most productive and largest amount of standing stock biomass for the benthos compared to any other region (Figure 4b, 5a).

There was a large consumptive demand on all small pelagics (Figure 5b). This was particularly so in the Gulf of Maine and on Georges Bank. All the intermediate trophic levels, at least pre-balanced, often had more consumptive demand than was produced. However, balancing tended to mitigate this by transferring lower trophic level production to these second, third or even fourth trophic levels and by lowering total amounts of consumption on these groups. These results highlight the high cumulative magnitude of predation on small pelagics, even more than other fish or invertebrates at similar trophic levels.
The entire ecosystem was 10 to 15 times more productive than what was removed by fisheries (Figure 6). Of the main fisheries, on an areal basis Southern New England produced the most landings relative to what the system produced. Demersals fisheries removed 10 to 15 times more than what the system produced across all regions (Figure 6b). Whereas pelagic fisheries only removed 2 to 6 times more than what the system produced across all regions, with the exception of Southern New England (Figure 6a). We infer from this that small pelagic fisheries were operating at a higher level in the more northern regions, particularly the Gulf of Maine.

There were 100 times more consumption of small pelagics in the Gulf of Maine than what was landed (Figure 6a). This ratio declined going south to Georges Bank to Southern New England to the Mid-Atlantic Bight, but the Mid-Atlantic still had 24 times more consumption than landings of small pelagics. The opposite trend was seen for the demersals (Figure 6b), with the ratio at about 60 times more in the Mid-Atlantic to about 40 times in the other regions. Clearly small pelagics were an important set of nodes for energy flux in this ecosystem. Overall, these ratios imply that biomass and energy removed from one node was driven more by internal system dynamics than external removals.

Scenarios

Changing the small pelagics exhibited obvious changes in that group. But interestingly these changes also produced compensation exhibited by all other fish groups (Figure 7a, 8a). That is, when small pelagics stocks were lowered, other fish were higher, and vice versa. The same was true for scenarios involving the demersals (Figure 7b, 8b).
However, the highly migratory species and sharks had a minimal effect on most other fish groups, except a slightly negative response in the larval and juvenile fish (Figure 7c, 8c). Surprisingly, there was minimal impact on small pelagic nodes in these scenarios. Changing the marine mammals resulted in a consistent and counter-intuitive increase in small pelagics (Figure 7d, 8d). In the EcoPath model, small pelagics increased, but in the EcoNetwrk model the small pelagics at a smaller rate and highly migratory species increased, except in the last scenario.

We also wanted to explore how these scenarios would trickle down to lower trophic levels. Overall, every scenario had a negative impact on gelatinous zooplankton and to a lesser degree macrobenthos (Figure 9, 10). We suspect that this may be a function of the high biomass initially sequestered in those nodes. It may also be more a function of the system structure and pathway “wirings” constructed in our models rather than a true dynamic of the system.

Interestingly, zooplankton biomass did not decrease in any scenario (Figure 9, 10). This was particularly counter-intuitive in scenarios where planktivore (i.e. small pelagics) biomass increased. Again, this may be more a function of how we constructed the energy budget and its component flows than a true dynamic of the system. It is likely that the tradeoff in zooplankton, shrimp, and micronekton versus gelatinous zooplankton may represent some form of compensation at the systemic level. Thus, overall there was minimal change in the second trophic level nodes (Figure 11, 12). In many ways these energy budgets were pre-balanced and the scenarios served to redistribute biomass and fluxes to similar nodes, primarily through subtle changes in diet composition of the predators. In some of the extreme scenarios when balancing in both EcoPath and
EcoNetwrk, efficiencies and various ratios were substantially altered such that the fundamental characteristics of a node were altered. These results suggest that instead of changing the biomass of a node as would obviously be expected, the properties of the organisms needed to adapt. Where these adaptations went beyond what is feasible is suggestive that although we achieved balance of the network, some structural caveats and misunderstandings of our ecosystem remain on our part.

**Discussion**

The EMAX exercise and the process of model balancing were informative in many respects, not least of which was highlighting areas where our perceptions or understanding may merit revising or re-examining when compared to this holistic view of the data, relative magnitudes of different nodes, or combined model outputs.

Small pelagics are an extremely important part of the NEUS ecosystem. It is likely that they are going to continue to be for the foreseeable future. A majority of energy in the system flows through these nodes. How other species, especially commercially or ecologically ones, respond to herring, mackerel, squids, and similar organisms remains an increasingly important issue. It appears that when the amount of small pelagics in the system changes, there are trickle through effects to other network nodes. In terms of biomass, production, energy flows, and importance for upper trophic levels, small pelagics are a keystone group of species in this ecosystem.

Total system production is less than primary production when one accounts for respiration, trophic transfer efficiencies, etc. Which begs the question, can we have optimized biomass for all groups simultaneously (sensu Larkin 1996, Link 2002)? This
remains a key question for global fisheries management and merits revisiting in additional exercises.

The system appears to be driven from bottom-up more than the top-down factors. This is one of the most productive marine ecosystems on the planet (Bax 1991, Cohen et al. 1982, Grosslein et al. 1980, Sissenwine et al. 1984), an observation reinforced by this study. As a proportion of primary production, most of the events at upper trophic levels are an extremely small fraction. More telling is that total fisheries catch is a low proportion of overall energy flow. Even when we increase the biomass of small pelagics by two orders of magnitude, the effects on the immediately next lower trophic level (i.e. zooplankton) are minimal. Further, given the connectedness of all the species in this ecosystem, it appears that if one energy pathway is altered, another pathway compensates such that overall changes in standing stock biomass at a given trophic level are minimized. These are all symptomatic of a highly productive and highly resilient system.

One thing that became obvious is that we needed to add in bacteria and microzooplankton (Azam et al. 1983) to “close the loop (model domain),” be more realistic, recognize current scientific developments, and balance the model. Dissolved organic carbon is likely the largest biomass node in the system, at least by several orders of magnitude. This represents a major change in thinking and philosophy of how the oceans work as compared to even 10-20 years ago. It has become clear that bacteria may be very important on a system scale. All of these observations point to the consideration that lower trophic level processes and biomasses are likely dominant in most marine ecosystems. But how exactly important they are in terms of driving the
system and scaling the magnitude of biomass for upper trophic levels remains a major unknown.

Another useful part of this exercise was that it helped us to identify data gaps (Table 2). Some of the major parameters of what turned out to be the most important nodes for ecosystem dynamics, structure and function were those at these lower trophic levels. As is likely the case, most of those nodes are under-resolved or unknown in many instances. Although we work for a fisheries agency, it is interesting to note that many of the organisms that ultimately drive fish production are at much lower trophic levels, typically not monitored or studied. Although the microbial loop, gelatinous zooplankton, and similar lower trophic levels can be extremely important in how an energy budget balances, their biomass and rate processes are difficult to estimate. Some groups like this are always going to be problematic or inherently underdetermined. Until clear advances in sampling and monitoring technology are developed and become routine, we may have to simply recognize that many of our efforts for estimating parameters associated with these types of groups simply provide a bounding of possible magnitudes.

A related point is that even in data rich systems (Fogarty and Murawski 1998, Link and Brodziak 2002) there are still data gaps. And in particular, rates continue to pose key challenges. A better catalog and compilation of common fisheries and marine ecological rates is warranted. Additionally, knowing the diet compositions of component organisms is paramount for energy budgets and network analyses. Without this information, there is no way to estimate flows between nodes. Getting the flows right is critical for this type of exercise. We were fortunate to have an extensive food habits
database (Link and Almeida 2000). Yet more can be done for fish (both here and globally) and certainly other species groups on this topic.

The differences across the software packages we examined are not trivial. Yet although the underlying models are quite different, the overall results were similar from the two main ones we used (EcoPath and EcoNetwrk). A similar study in the Benguela ecosystem also highlighted some of the key differences and similarities that we observed (Heymans and Baird 2000). The point is that there is value in multiple modeling approaches (Whipple et al. 2000). In particular, this broader framework allowed for feedback between the models and input matrices, which was important to be able to iterate.

Obviously there is a lot more we could elaborate on from this set of work. Space and time here preclude us from presenting and examining all the possible contrasts and insights to be gleaned from this work. In particular, future work should initially consist of more detailed examinations of a broader set of cybernetic and systems metrics. Comparing the results of the contemporary study to some historical energy budgets from this region (Cohen et al. 1982, Grosslein et al. 1980, Sissenwine et al 1984,) will also be valuable. We recognize that the current work is singularly focused on the NEUS ecosystem, but that much similar work has been executed around the globe (e.g. Bundy 2005, Christensen and Pauly 1992, 2004). Comparative studies exploring the differences and similarities among these different marine ecosystems will better elucidate key marine and fisheries processes, patterns, and theories. This is particularly feasible given an increasingly common set of standard network, cybernetic, and ecological metrics which integrate a wide range of information for a system. Additionally, further comparisons
across the four sub-regions, more detailed analyses between the two (and perhaps other) model outputs, exploring other statistics, and more rigorous and formal scenario testing will allow us to even further elucidate the key dynamics of the NEUS ecosystem.

There is an ever-increasing need for holism in marine and fisheries science (Jorgensen 1992, Link 2002). One of the values of an exercise like this is gaining a better sense of the relativity of concurrent processes. That the dynamics of this and likely most marine ecosystems are dominated by the first two trophic levels is a sober reminder that the relative magnitude of important events and processes may often be beyond human control. Yet at the same time, our ability to even detect changes in network nodes that are often highly influenced by human events in marine systems (e.g. fishing) is critical. Being able to evaluate such events in the context of an entire system is going to be an increasingly important task as we move towards EAF/EBFM (Garcia et al. 2003, Garcia 2005, Link 2002).

Doing EAF/EBFM is not going to be easy, but it is feasible. Several of the positive outcomes from the EMAX exercise are obvious. Yet others are more sublime, including some fundamental shifts in underlying philosophies of fisheries science and fisheries institutions. More pragmatically, EMAX and projects like it will continue to play a critical role for the further development of EAF, particularly as: a catalogue of information and data; identifying major fluxes among biotic components of the ecosystem; a basis for further analytical models; a way to evaluate biomass tradeoffs; and a backdrop for a suite of other relevant, management and research questions.
Acknowledgements

We thank a lot of people who over half a century have designed, collected and maintained what are in many respects some premier datasets for the NEUS portion of the world’s ocean environment. We thank the NESFC executive staff who allowed all of us to dedicate a portion of our time to this exercise despite its high risk.
Literature Cited


Table 1. Various scenarios tested by EMAX, in the Gulf of Maine region. The factor represents by how much the noted node groups were multiplied. The scenarios were balanced using both EcoPath and EcoNetwrk software packages.

<table>
<thead>
<tr>
<th>Baseline</th>
<th>Factor</th>
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<td>10</td>
</tr>
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<td></td>
<td>100</td>
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<td>1/10</td>
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<td>10</td>
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Table 2. Data “pedigree” for all nodes modeled in EMAX. Lower numbers or bluer colors are less certain/resolved estimates, higher numbers or redder colors are more confident estimates. Modified from a similar EcoPath module. B = Biomass, P/B = production, Q/B = consumption, Diet = diet composition, Catch = landed removals.

<table>
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<th>B</th>
<th>P/B</th>
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<th>Diet</th>
<th>Catch</th>
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Figure Captions.

Figure 1. Map of the Northeast U.S. continental shelf large marine ecosystem, with four subregions highlighted. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight.

Figure 2. General network used for EMAX. Each node can represent a wide range of taxa. Flows between nodes are not shown for the sake of clarity.

Figure 3. A. Biomass ratios of other upper trophic levels relative to small pelagics. B. Biomass ratios of various invertebrate groups, relative to one another and small pelagics. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. ZP = zooplankton, PP = primary producers.

Figure 4. A. Percent of total fish biomass comprised by various groups. B. Percent of total invertebrate biomass comprised by various groups. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. ZP = zooplankton.

Figure 5. A. Production ratios of various invertebrate groups, relative to one another and primary production. B. The amount consumed relative to the amount produced for various fish and invertebrate groups. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. ZP = zooplankton, PP = primary producers.

Figure 6. Ratio of production (P) and consumption (C) to landings (L) for A. Small pelagics and B. Demersals. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight.
Figure 7. Percent change in the percentage of total fish biomass for the various levels
(1/100, 1/10, \( \frac{1}{2} \), 2, 10, and 100 \times\) original biomass value) of each major scenario, as
estimated by EcoPath. A. Changing small pelagics scenario. B. Changing demersal fish
scenarios. C. Changing highly migratory species and sharks scenarios. D. Changing
marine mammals scenario. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern
New England, MAB = Mid-Atlantic Bight.

Figure 8. Percent change in the percentage of total fish biomass for the various levels
(1/100, 1/10, \( \frac{1}{2} \), 2, 10, and 100 \times\) original biomass value) of each major scenario, as
estimated by EcoNetwrk. A. Changing small pelagics scenario. B. Changing demersal
fish scenarios. C. Changing highly migratory species and sharks scenarios. D. Changing
marine mammals scenario. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern
New England, MAB = Mid-Atlantic Bight.

Figure 9. Percent change in the percentage of total invertebrate biomass for the various
levels (1/100, 1/10, \( \frac{1}{2} \), 2, 10, and 100 \times\) original biomass value) of each major scenario, as
estimated by EcoPath. A. Changing small pelagics scenario. B. Changing demersal fish
scenarios. C. Changing highly migratory species and sharks scenarios. D. Changing
marine mammals scenario. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern
New England, MAB = Mid-Atlantic Bight. ZP = zooplankton.

Figure 10. Percent change in the percentage of total invertebrate biomass for the various
levels (1/100, 1/10, \( \frac{1}{2} \), 2, 10, and 100 \times\) original biomass value) of each major scenario, as
estimated by EcoNetwrk. A. Changing small pelagics scenario. B. Changing demersal fish
scenarios. C. Changing highly migratory species and sharks scenarios. D. Changing

Figure 11. Percent change in biomass ratios of various invertebrate groups for the various levels (1/100, 1/10, ½, 2, 10, and 100 x original biomass value) of each major scenario, as estimated by EcoPath. A. Changing small pelagics scenario. B. Changing demersal fish scenarios. C. Changing highly migratory species and sharks scenarios. D. Changing marine mammals scenario. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. ZP = zooplankton.

Figure 12. Percent change in biomass ratios of various invertebrate groups for the various levels (1/100, 1/10, ½, 2, 10, and 100 x original biomass value) of each major scenario, as estimated by EcoNetwrk. A. Changing small pelagics scenario. B. Changing demersal fish scenarios. C. Changing highly migratory species and sharks scenarios. D. Changing marine mammals scenario. GoM = Gulf of Maine, GB = Georges Bank, SNE = Southern New England, MAB = Mid-Atlantic Bight. ZP = zooplankton.
Figure 4

A

% of Total Fish Biomass

- Small Pelagics
- Demersals + Med Pel
- HMS + Sharks
- Larval + Juv Fish

B

% of Total Invertebrate Biomass

- ZP
- Shrimp + Micronekton
- Macrobenthos
- Megabenthos
- Gelatinous ZP

GOM | GB | SNE | MAB
---|---|---|---

Figure 6

A) Small Pelagics

B) Demersals

Legend:
- Production/Landings
- Consumption/Landings
Figure 7

A

Ecopath, Small Pel

B

Ecopath, Demersals

C

Ecopath, HMS

D

Ecopath, Mammals

% Change in % of Total Fish Biomass

-150% -100% -50% 0% 50% 100% 150% 200% 250%

1/100 1/10 1/2 2 10 100

% Change in % of Total Fish Biomass

-200% 0% 200% 400% 600% 800% 1000%

100 1/100 1/10 1/2 2 10

% Change in % of Total Fish Biomass

-30% -20% -10% 0% 10% 20% 30% 40%

1/100 1/10 1/2 2 10 100
Figure 11

A. Ecopath, Small Pel
- Shrimp + Micronekton / ZP Biomass
- Benthos / All ZP + Micronekton

B. Ecopath, Demersals
- Shrimp + Micronekton / ZP Biomass
- Benthos / All ZP + Micronekton

C. Ecopath, HMS
- Shrimp + Micronekton / ZP Biomass
- Benthos / All ZP + Micronekton

D. Ecopath, Mammals
- Shrimp + Micronekton / ZP Biomass
- Benthos / All ZP + Micronekton