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A Model of Aggregate Biomass Tradeoffs

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Abstract

Multi-species and ecosystem based approaches to fisheries management provide alternate and complimentary views of fishery ecosystems. This work provides an example of the need to consider species interactions when evaluating and establishing management goals. Given the caveats of scale and variability, there is a finite amount of biological production within ecosystems. These carrying capacity limits to all levels of biomass production can lead to difficult choices about the allocation of production and biomass among commercially valuable finfish. I present a model based upon the functional guild approach to explore various scenarios for a hypothetical food web, roughly analogous to the finfish community of the U.S. northwest Atlantic. The model, an extension of simpler production models, has both ecological and abiotic constraints and accounts explicitly for predation, competition, and harvest. Model simulations show greater stability of biomass at the guild level when compared to the species level, irrespective of species composition within a guild. Individual species biomasses within a guild are typically much more dynamic. Fishing and abiotic conditions are the more dominant factors changing total guild biomass when compared to internal ecological dynamics. Scenarios with excessive fishing demonstrate a tendency to forego biomass relative to the potential carrying capacity in an ecosystem. These simulations mimic observations of the U.S. northwest Atlantic finfish community from the past 40 years. Using aggregate models such as the one presented here will generally provide more conservative harvest reference points and are likely to be valuable tools for further implementation of the precautionary approach.

KEYWORDS: guild, trophic dynamics, production models, multi-species, reference points, fishery management

Introduction

From the second law of thermodynamics we know there is a finite amount of energy and biomass. In any given system this is true, but transports to and from the system also need consideration since no system is totally closed. Energy and mass can only be converted or moved, not destroyed or created. Applied in an ecological sense, Elton (1927) described the pyramid of energy for food webs, within which there are energetic constraints for subsequent trophic levels (Lindeman 1942).

The northeast U.S. continental shelf is an open and dynamic ocean system where subarctic, temperate, and subtropic nutrients, water current regimes, thermal energies, and species mix. Accounting for cycles, inherent variability, fluxes, removals or additions to the energy of this ecosystem, for any period of time there is a fixed amount of energy available for conversion to biomass. An illustrative example is that regardless of species composition, phytoplankton and zooplankton biomass has remained relatively consistent across the past several decades on Georges Bank (O'Reilley and Zetlin 1998, Sherman et al. 1996). After considering directed removals, changes in production rates, and changes in migration patterns, it is reasonable to presume that the consistency of energy converted to biomass by the phytoplankton and zooplankton has transferred to upper trophic levels, providing approximate bounds for the biomass of these consumers. It is also reasonable to presume that the species composition of these upper trophic levels are not necessarily constant; Georges Bank and vicinity have exhibited notable shifts in the fish assemblage over the past few decades (Fogarty and Murawski 1998, NEFSC 1999). In particular, once dominant gadids and flatfish were replaced in the 1990s by elasmobranchs and small pelagic fishes.

Regardless of whether the absolute amount is fixed or varies across decades, at any given time there is a limited amount of energy available on Georges Bank and vicinity. Brown et al. (1976) asserted that the sum of MSY for multiple species will always be greater than the system MSY. It is apparent that simultaneously maximizing MSY for multiple species, even for just all managed species in a food web, is unfeasible, and leads to some hard choices about the particular species composition to be allocated from the total biomass of an ecosystem. Tradeoffs in biomass among species merit further examination.

However, there are few models designed to directly accommodate biomass tradeoffs, particularly in a fisheries management setting. Here I provide a model of biomass tradeoffs to better evaluate a suite of various scenarios. The model is based upon the functional guild approach and is roughly analogous to the finfish community of the U.S. northwest Atlantic. This model quantitatively evaluates tradeoffs in biomass among constituent species observed after differential perturbations to the fish community.

Methods

Recall a Schaeffer production model (Schaeffer 1954):

$$\frac{dB}{dt} = rB(1 - \frac{B}{k}) - qEB \qquad \text{EQ. 1}$$

where B is biomass, r is the intrinsic growth rate, k is the carrying capacity, and q (catchability) E (fishing effort) B is the fishery harvest of the species. Modifying this equation to account for multiple species, so that each species i belongs to a particular guild g, we can rewrite the equation to include both intra-guild competition, between guild competition, predatory removal, and fishery harvest, resulting in:

$$\frac{dB_i}{dt} = r_i B_i \cdot (1 - \frac{B_i + \sum_1^g b_{ig} B_g}{(K_g + gT)} - \frac{\sum_1^G b_{iG} B_G}{(K_s - K_g)} - \sum_1^p a_{ip} B_p) - (H_i \cdot B_i) \qquad \text{EQ. 2}$$

where again B (or N) is biomass (or can be expressed in numerical abundance), *g* is the number of individual species in a guild (or reference to a particular guild), *i* is an individual species, and *r* is the intrinsic growth rate. β (Beta) is the competition coefficient, and α (alpha) is the predation coefficient for all predators *p*. *K* is the carrying capacity of either guild *g* or the entire system σ (sigma), with temperature (*T*) corrected coefficient (γ; gamma) to allow for climate induced changes in growth. *G* is the total number of all guilds, *H* is the fishery harvest rate and *t* is time.

The model was initially constructed with five major guilds (*G*) and five species per guild, with a total of 25 species in the model. These five guilds represent the major trophic guilds of Georges Bank and associated waters (Garrison and Link 2000a, b) and were chosen to represent benthivores, planktivores, shrimp-amphipod feeders, shrimp-fish feeders, and piscivores. The initial parameterization was set up so that there was a distinct hierarchy of competitive dominance and predator avoidance within each guild, usually with the first species in a guild most dominant. The initial biomass in each guild was set as equal for each species, and the base scenario was run and parameterized to ensure local model stability (Table 1). The total system carrying capacity was set at 200 biomass units, similar to the long term average of total organism biomass from the NEFSC bottom trawl survey (Figure 1; Link and Brodziak 2002). These were allocated among the different guilds with some recognition that ultimate lower biomass resides in upper trophic levels (Table 2).

The model was parameterized with basal coefficients (Table 1) and run for 30 time steps, roughly analogous to 30 years. The model was integrated using a second order Euler method. The parameterization accounted for different degrees of intrinsic growth rates, within guild competition, between guild competition, predation, temperature influences on carrying capacity, and predator carrying capacity limited by trophic constraints. The results of the various model runs were evaluated by guild, aggregate groups (e.g., demersal or pelagic) and species. The model was and can be run for multiple scenarios including climate change, species extinction, or overfishing. Here I only present results of different overfishing scenarios, which were modeled by alternating the harvest rate for a given scenario. The main scenarios examined were: 1) the base model, 2) all demersals overfished; 3) all pelagics overfished; 4) the piscivore guild overfished; 5) the benthivore guild overfished; 6) the planktivore guild overfished; 7) both shrimp feeding guilds overfished; and 8) when only the dominant species in each guild is overfished.

Results

The base scenario generally shows, by design and parameterization, stability (with respect to total conservation of energy/mass) over the time frame modeled (Figure 2). This scenario exhibits total system biomass stability and stability of guild biomass, generally reflective of initial conditions. However, species composition within guilds change notably (Figure 3), with the dominant species strongly outcompeting other species within a guild.

The first scenario, overfishing demersals, shows an obvious decline in most guilds except the planktivore guild (Figure 4). The other four guilds have lower biomass than initial conditions or compared to the base scenario, mostly due to direct effects of fishing harvest. Probably the most interesting emergent property from this model output is the total system biomass is about one half of the carrying capacity under this scenario compared to the base case scenario.

The second scenario, overfishing pelagics, shows a notable decline in planktivores, and a less obvious decline in both shrimp feeding guilds (Figure 5). Also, the shrimp-fish feeding guild and the piscivore guild exhibit less biomass than the base case scenario principally because there is less food for these two guilds to eat. As in the prior scenario, four of the five guilds are effected but only two directly so. The total system biomass is about three-fourths of the base case scenario.

The third scenario, overfishing piscivores, shows a notable decline in piscivores due to direct harvest (Figure 6). The shrimp-fish feeding guild also exhibits a decline due to direct effects of fishery harvest. However, the other guilds compensate and the total system biomass is similar to the base case scenario. This constancy of system biomass is an example of predatory release akin to the fishing down the web hypothesis (Pauly et al. 1998).

The fourth and fifth scenarios, overfishing benthivores and planktivores, both exhibit a decline the respective guilds (Figures 7, 8). When one guild is fished down, the other tends to take its place (and vice versa). Yet there is a minimal positive, competitive response among the shrimp feeding guilds, likely due to the removal of some forage base for higher trophic level species in these guilds and thus increased competition with the top piscivores. The total system biomass in both these scenarios is about three-fourths the base case scenario.

The sixth scenario, overfishing shrimp feeders, is an intriguing case (Figure 9). In this scenario, both of the shrimp feeding guilds notably decline compared to the base case scenario, but the benthivores and planktivores exhibit a positive competitive response and essentially take the place of the shrimp feeding fish. The response by the top predators (i.e., piscivores) is nil, mainly because the forage base remains adequate. Total system biomass at the end of the simulation is almost at system carrying capacity.

The final scenario, overfishing just the dominant species in each guild, nearly mimics the base case scenario (Figure 10). Most guilds are stable and total system biomass is at or near carrying capacity. However, the dominant species in each guild is fished to very low levels, which, as one would expect, allows the competitive inferior species to increase in abundance (Figure 11).

Discussion

The model results are very similar to what we actually observed in the northeast U.S. continental shelf ecosystem (Fogarty and Murawski 1998, NEFSC 1999, Link and Brodziak 2002). There has been reasonable constancy in total system biomass yet notable changes in both species and guild composition, probably some combination most similar to the overfishing piscivores, demersals, or shrimp feeding guild scenarios. These scenarios compare favorably to what we know of the general fishing history in this ecosystem. Being able to reasonably replicate patterns and trajectories in observed data with this model is a positive and non-trivial result. Not that all the probable mechanisms and processes operating on Georges Bank have been entirely and adequately captured, but many of the key elements appear to have been replicated from this set of modeling exercises.

Another major benefit derived from this model is that it allows one to evaluate directly tradeoffs in biomass within the ecosystem in a relatively simple and straight forward fashion. Certainly there are other models extant to explore biomass tradeoffs (e.g., MSVPA, Ecopath, etc.; Hallowed et al. 2000, Whipple et al. 2000), yet those are typically much more data and parameter intensive. Using this model as a modification of the highly vetted Schaeffer class of models will also allow one to bring a suite of related methodologies and modeling tools to calculate common reference points, uncertainty indices, and sensitivity analyses for a variety of projections and scenarios. The value of using this model as an extension of the single species Schaeffer approach is that not only do we obtain outputs that are well known in fisheries situations, but we can also begin to address the central issue of biomass tradeoffs.

Three general conclusions arise from the results of this model. First, the "equilibrium" guild biomass is relatively stable, but the individual species biomass within a guild is very dynamic. Second, over-fishing different guilds or aggregate groups in whatever category may result in foregone yield relative to overall systemic carrying capacity. Finally, external perturbations are more important than internal dynamics with respect to changing guild biomass.

There are also three corollary points to remember when considering biomass tradeoffs for a fishery ecosystem. First is that biomass will end up somewhere in the food web as a result of our harvesting activities, and it might not be in species we value. Ecological or functional equity does not necessarily translate into market equity. Second, to maximize long term economic yield and given ecological constraints, it appears wise to allow for some diversity of biomass in and among guilds. Given the natural and edaphic perturbations to most marine food webs, it is unlikely that competitive exclusion will ever be fully realized within a guild. Yet perhaps B_{MSY} set at $K/2$ would be more conservatively set if we used *K* at the guild or system level. Finally, we assume we can direct the response of an ecosystem towards a particular end when in fact it is unclear if that is possible for such a complex, open ecosystem like Georges Bank (Larkin 1996, Link 1999). We need to remember that we may desire a certain biomass tradeoff, but we will likely have little if any control over the ecosystem to obtain this result. The best we can do is manage biomass in accordance with our understanding of how the ecosystem functions and hope the system responds in a manner in which we would like.

Although not presented formally here, it is clear that accounting for species interactions such as in this model will lower biological reference points. This is a generality of all multispecies models, such that they all result in more conservative estimates of biomass projections (sensu Hallowed et al. 2000, sensu Whipple et al. 2000). Although potentially unpalatable in the short term, in the long term accounting for these interactions and adjusting our management actions accordingly will allow for higher sustainable yields much closer to the carrying capacity of a system than the lower and foregone yields experienced by most fishery ecosystems.

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Table 1. Parameterization of the basal model. B= benthivore guild, PL= planktivore guild, SA= shrimp-amphipod feeding guild, SF= shrimp-fish feeding guild, PI= piscivore guild. In the binary code for demersal or pelagic, 0= no, 1= yes.

	B1	B2	B3	B4	B5	PL1	PL2	PL3	PL4	PL5	SA1	SA2	SA3	SA4	SA5
Growth Rate	0.08	0.08	0.06	0.04	0.02	0.1	0.1	0.06	0.04	0.02	0.06	0.04	0.04	0.02	0.02
Initial Biomass	10	10	10	10	10	10	10	10	10	10	8	8	8	8	8
Competition Coefficient															
with Guild member 1	0	0.5	0.6	0.6	0.6	0	0.5	0.6	0.6	0.6	0	0.5	0.6	0.6	0.6
with Guild member 2	0.3	0	0.5	0.5	0.5	0.3	0	0.5	0.5	0.5	0.3	0	0.5	0.5	0.5
with Guild member 3	0.2	0.4	0	0.5	0.5	0.2	0.4	0	0.5	0.5	0.2	0.4	0	0.5	0.5
with Guild member 4	0.2	0.4	0.5	0	0.4	0.2	0.4	0.5	0	0.4	0.2	0.4	0.5	0	0.4
with Guild member 5	0.1	0.1	0.2	0.2	0	0.1	0.1	0.2	0.2	0	0.1	0.1	0.2	0.2	0
Temperature Coefficient	- 0.1	-0.1	-0.1	0	0	0.8	0.8	0.4	0.2	0.1	0	0	0	0.2	0.2
Predatory Loss rate															
with PI1	0	0.01	0.01	0.01	0.01	0.05	0.05	0.05	0.01	0.01	0.05	0.05	0.05	0.01	0.01
with PI2	0	0.01	0.01	0.01	0.01	0.01	0.05	0.05	0.01	0.01	0.01	0.01	0.01	0.01	0.01
with PI3	0	0	0	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0	0	0	0.01	0.01
with PI4	0	0	0	0	0.01	0	0.01	0.01	0.01	0.01	0	0	0	0.01	0.01

with PI5	0	0	0	0	0.01	0	0.01	0.01	0.01	0.01	0	0	0	0	0
with SF1	0	0	0	0	0.01	0.005	0.005	0.005	0.005	0.01	0	0.01	0.01	0.01	0.02
with SF2	0	0	0	0	0	0.005	0.005	0.005	0.005	0.01	0	0.01	0.01	0.01	0.02
with SF3	0	0	0	0	0	0.001	0.001	0.005	0.005	0.01	0	0.01	0.01	0.01	0.02
with SF4	0	0	0	0	0	0.001	0.001	0.005	0.005	0.01	0	0.01	0.01	0.01	0.02
with SF5	0	0	0	0	0	0	0.001	0.001	0.001	0.01	0	0.01	0.01	0.01	0.02
Competition Coefficient 2															
between Guild & Guild B	0	0	0	0	0	0	0	0	0	0	0.6	0.6	0.6	0.6	0.6
between Guild & Guild PL	0	0	0	0	0	0	0	0	0	0	0.4	0.4	0.4	0.4	0.4
between Guild & Guild SA	0.8	0.8	0.8	0.8	0.8	0.3	0.3	0.3	0.3	0.3	0	0	0	0	0
between Guild & Guild SF	0.5	0.5	0.5	0.5	0.5	0.2	0.2	0.2	0.2	0.2	0.5	0.5	0.5	0.5	0.5
between Guild & Guild PI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Demersal	1	1	1	1	1	0	0	0	0	0	1	1	1	0.5	0.5
Pelagic	0	0	0	0	0	1	1	1	1	1	0	0	0	0.5	0.5

	SF1	SF2	SF3	SF4	SF5	PI1	PI2	PI3	PI4	PI5
Growth Rate	0.08	0.08	0.04	0.04	0.02	0.04	0.04	0.02	0.02	0.01
Initial Biomass	8	8	8	8	8	4	4	4	4	4
Competition Coefficient										
with Guild member 1	0	0.5	0.6	0.6	0.6	0	0.5	0.6	0.6	0.6
with Guild member 2	0.3	0	0.5	0.5	0.5	0.3	0	0.5	0.5	0.5
with Guild member 3	0.2	0.4	0	0.5	0.5	0.2	0.4	0	0.5	0.5
with Guild member 4	0.2	0.4	0.5	0	0.4	0.2	0.4	0.5	0	0.4
with Guild member 5	0.1	0.1	0.2	0.2	0	0.1	0.1	0.2	0.2	0
Temperature Coefficient	- 0.2	-0.2	-0.2	0.1	0.1	0	0	0	0.1	0.2
Predatory Loss rate										
with PI1	0.05	0.05	0.05	0.01	0.01	0	0.01	0.01	0.01	0.01
with PI2	0.01	0.01	0.01	0.01	0.01	0	0	0.001	0.01	0.01
with PI3	0	0	0	0.01	0.01	0	0	0	0.001	0.001
with PI4	0	0	0	0.01	0.01	0	0	0	0	0
with PI5	0	0	0	0	0	0	0	0	0	0

with SF1	0	0	0	0.01	0.01	0	0	0	0	0
with SF2	0	0	0	0.01	0.01	0	0	0	0	0
with SF3	0	0	0.01	0.01	0.01	0	0	0	0	0
with SF4	0	0	0.01	0.01	0.01	0	0	0	0	0
with SF5	0	0	0.01	0.01	0.01	0	0	0	0	0
Competition Coefficient 2										
between Guild & Guild B	0.2	0.2	0.2	0.2	0.2	0	0	0	0	0
between Guild & Guild PL	0.2	0.2	0.2	0.2	0.2	0	0	0	0	0
between Guild & Guild SA	0.4	0.4	0.4	0.4	0.4	0	0	0	0	0
between Guild & Guild SF	0	0	0	0	0	0.4	0.4	0.4	0.4	0.4
between Guild & Guild PI	0.4	0.4	0.4	0.4	0.4	0	0	0	0	0
Demersal	1	1	0.5	0.5	1	1	1	1	0	0
Pelagic	0	0	0.5	0.5	0	0	0	0	1	1

Table 2. Carrying capacities (*K*) for each guild in the model.

Guild	K
Piscivores	20
Shrimp-Fish	40
Shrimp-Amphipods	40
Benthivores	50
Planktivores	50
Total	200

Figure 1. A. Long term average and time series of total organism biomass from the NEFSC bottom trawl survey. Units are in kg per tow and include all areas of the U.S. northwest Atlantic.

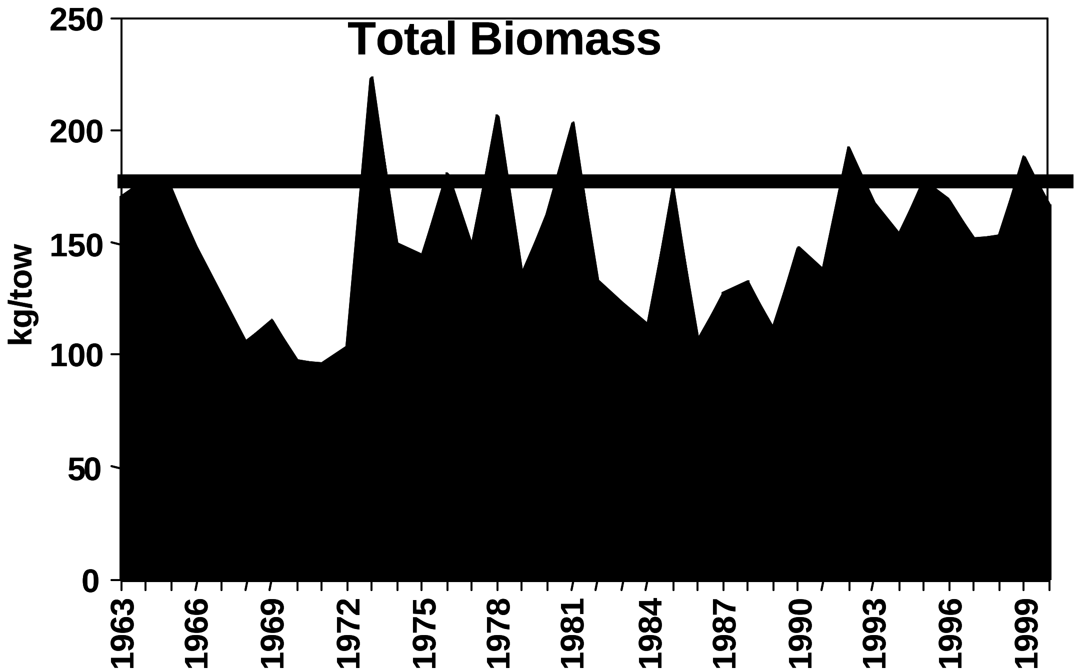
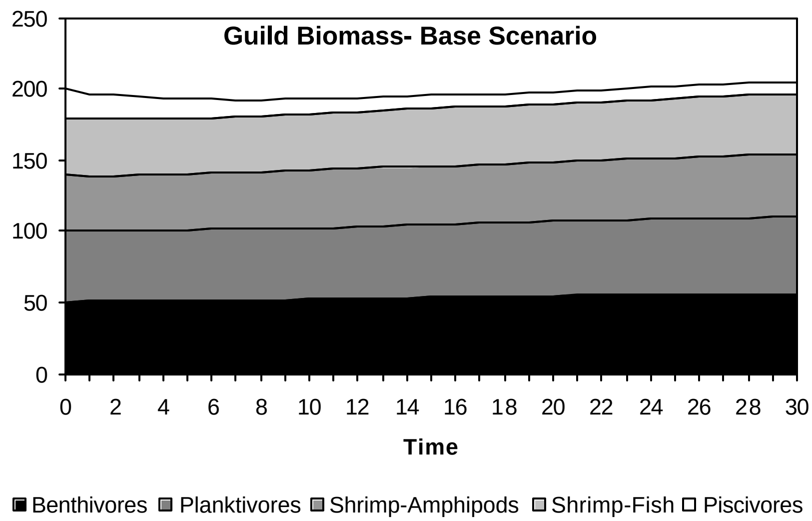


Figure 2. The base case run of the model. A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



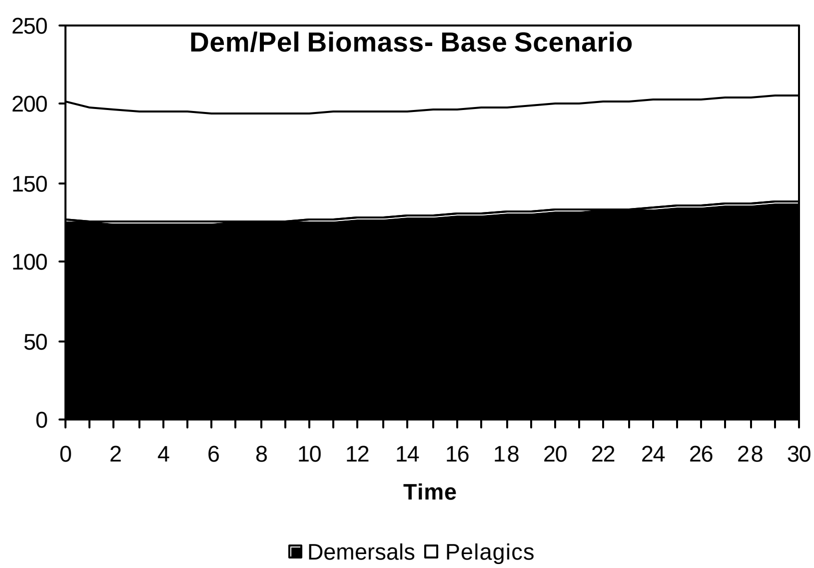


Figure 3. Single species trajectory for each member of a guild under the base scenario. A. Benthivores. B. Planktivores. C. Shrimp-amphipod feeders. D. Shrimp-fish feeders. E. Piscivores.

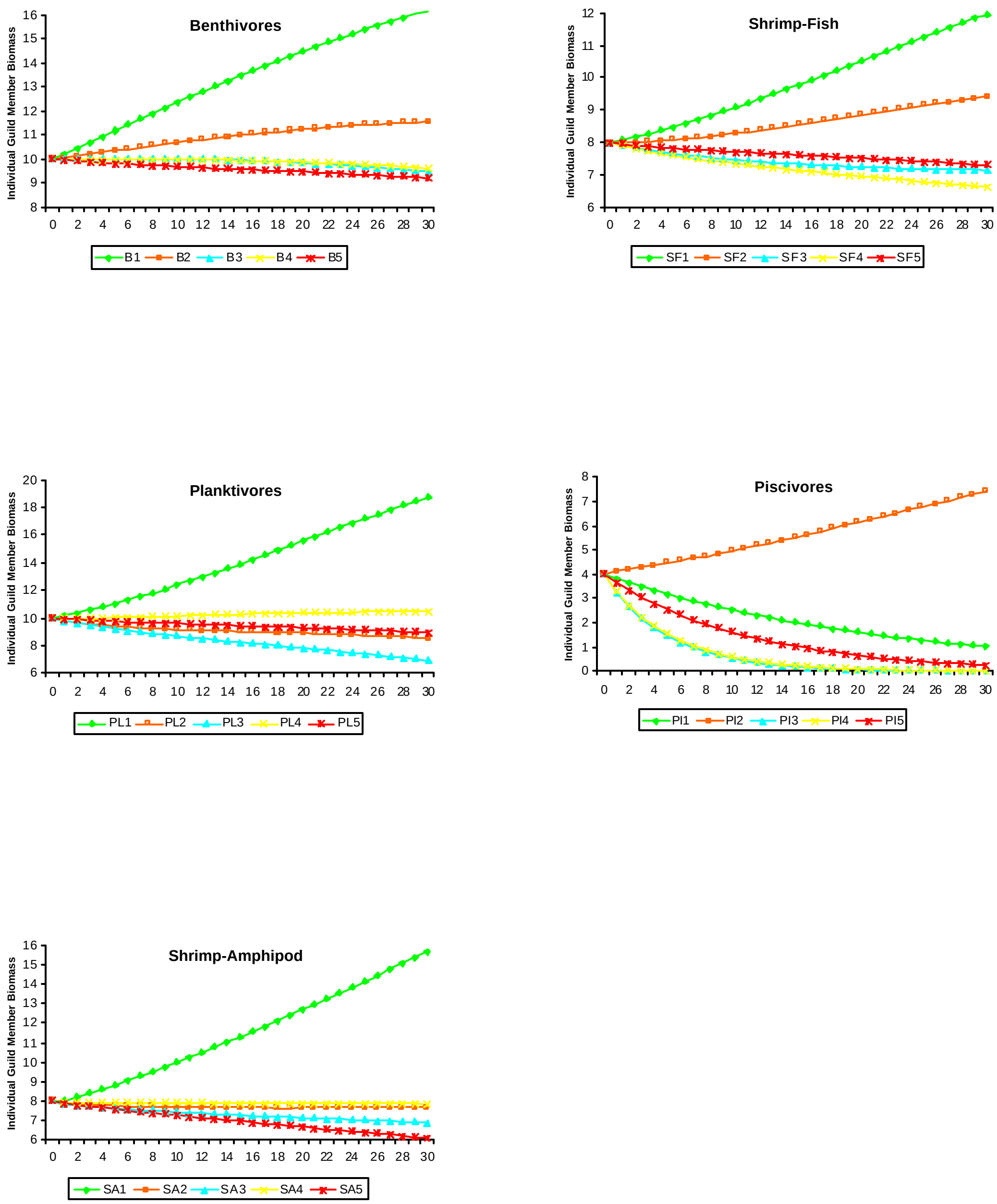
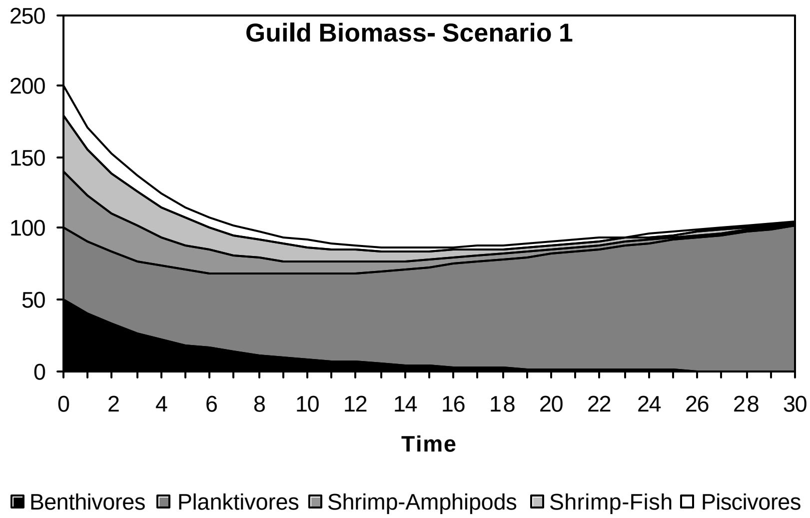


Figure 4. The results of the first scenario of the model, overfishing demersals. A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



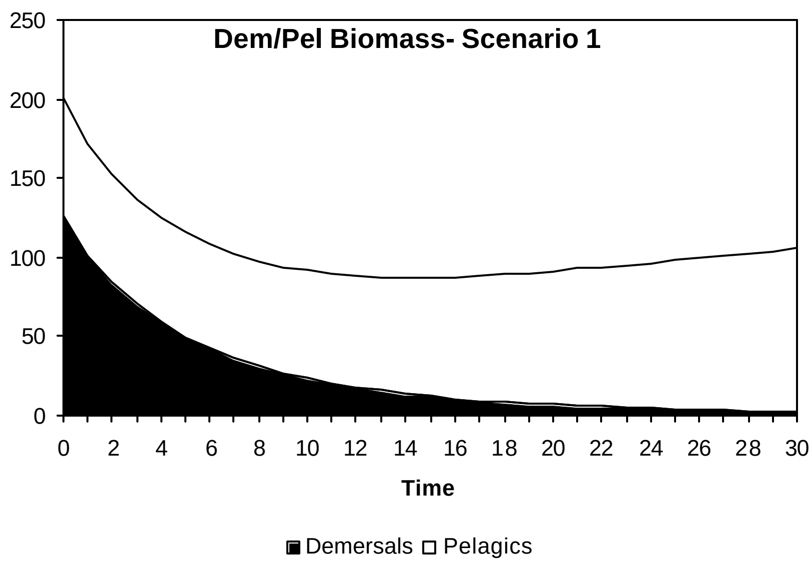
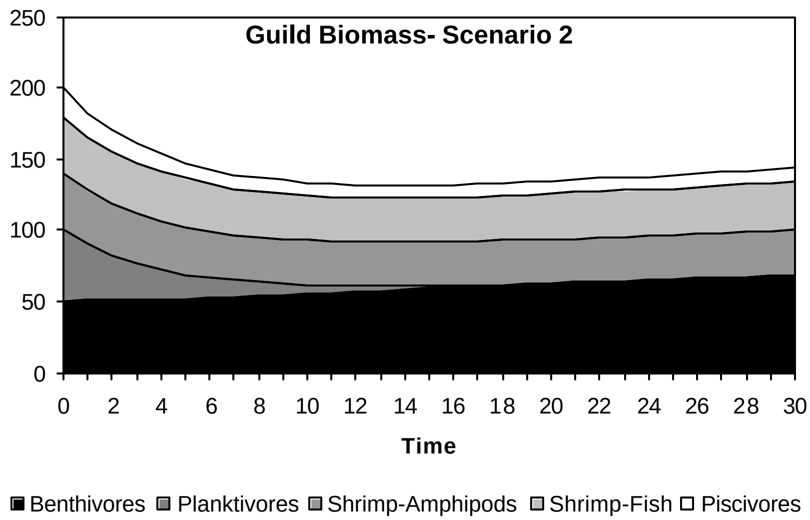


Figure 5. The results of the second scenario of the model, overfishing pelagics. A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



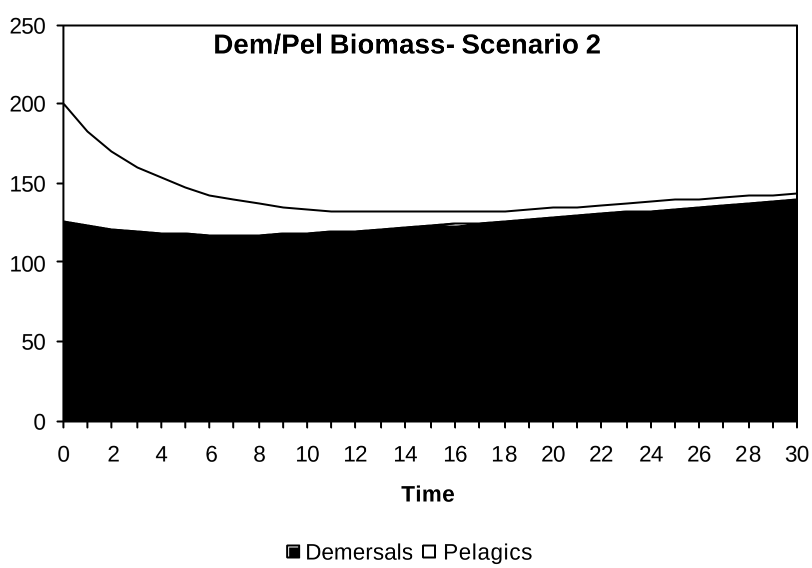
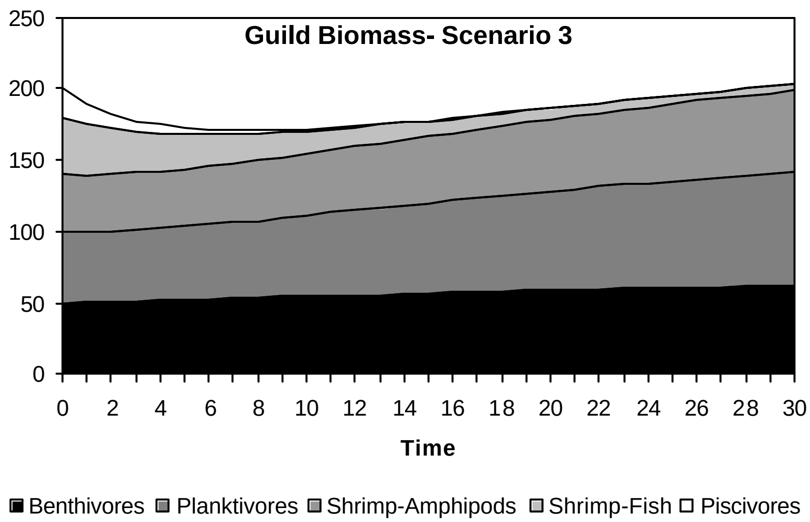


Figure 6. The results of the third scenario of the model, overfishing piscivores. A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



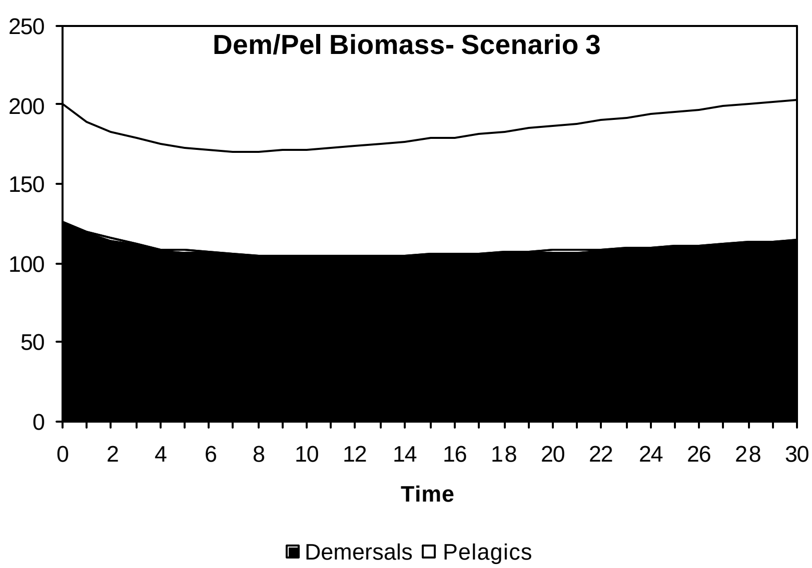
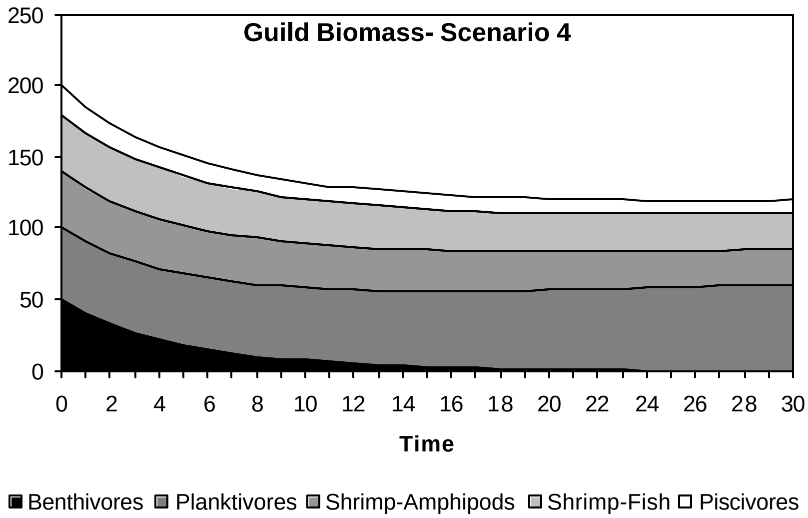


Figure 7. The results of the fourth scenario of the model, overfishing bentivores. A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



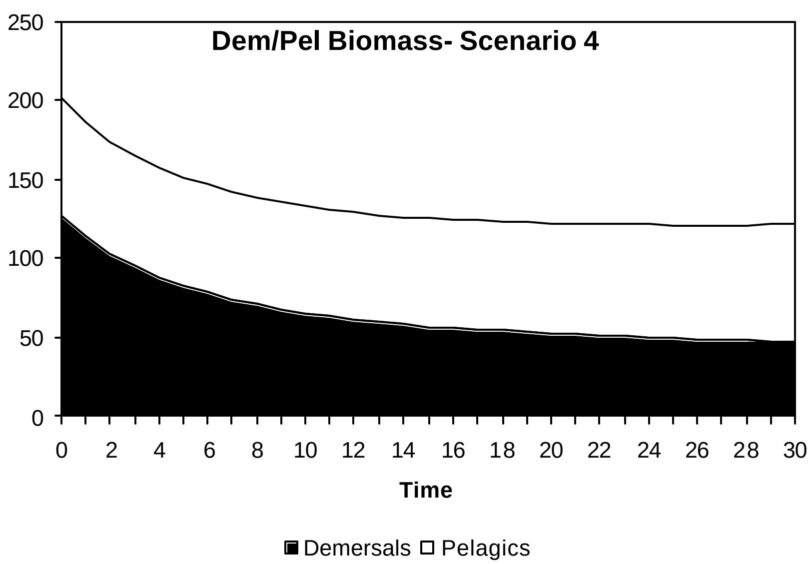
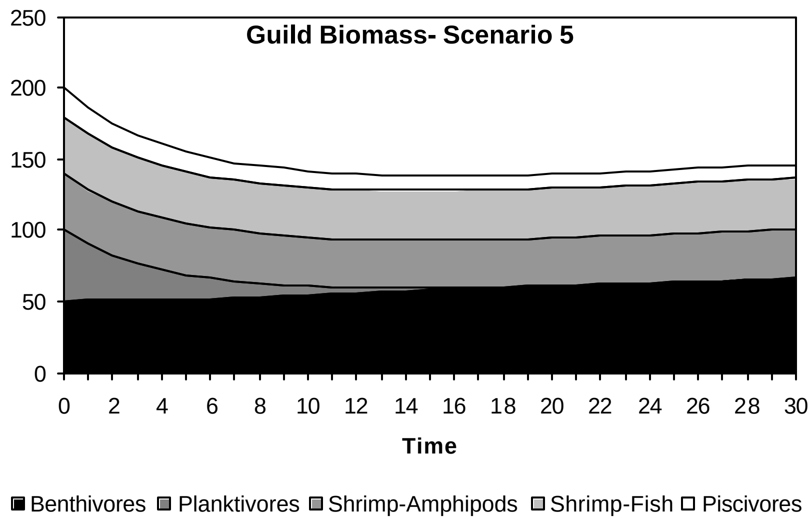


Figure 8. The results of the fifth scenario of the model, overfishing planktivores. A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



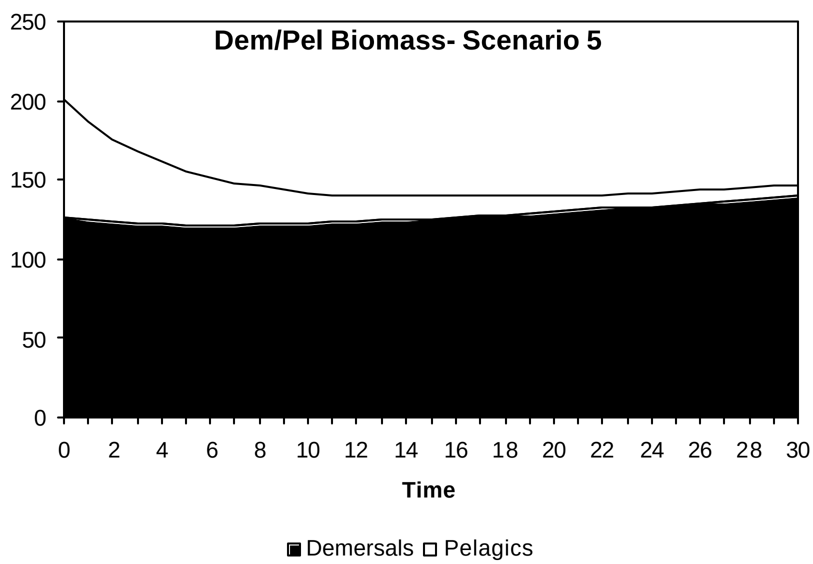
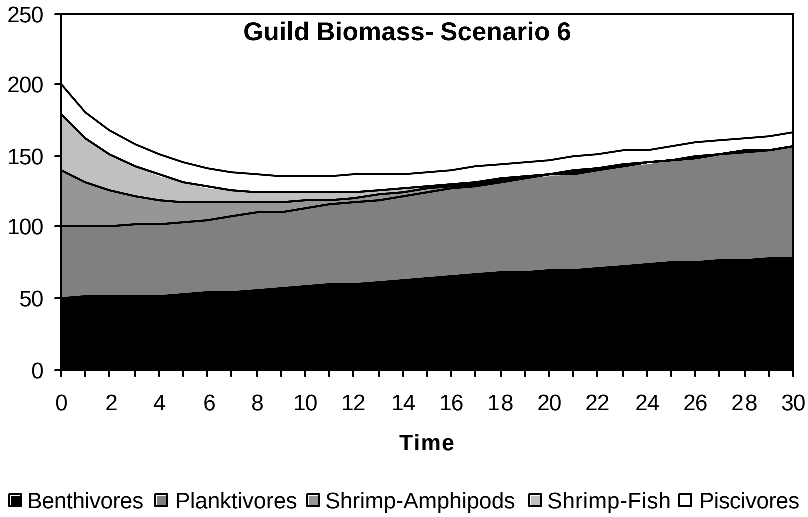


Figure 9. The results of the sixth scenario of the model, overfishing shrimp feeding guilds. A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



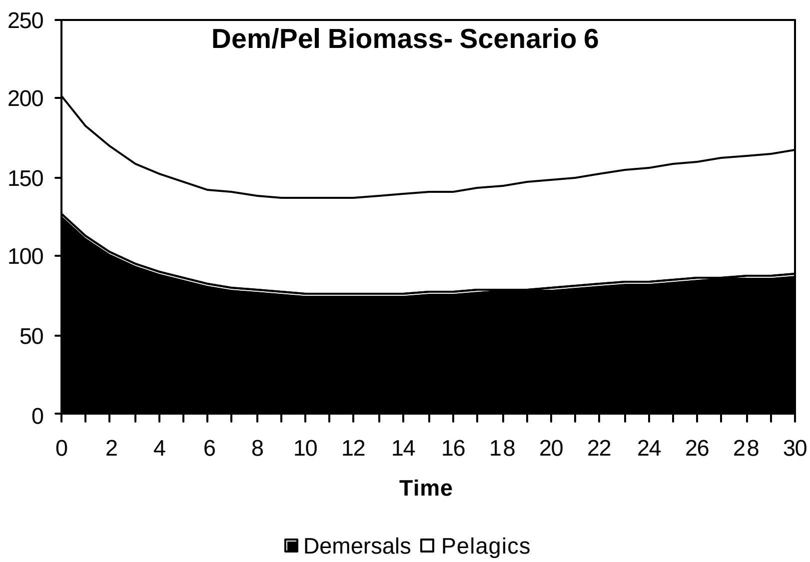
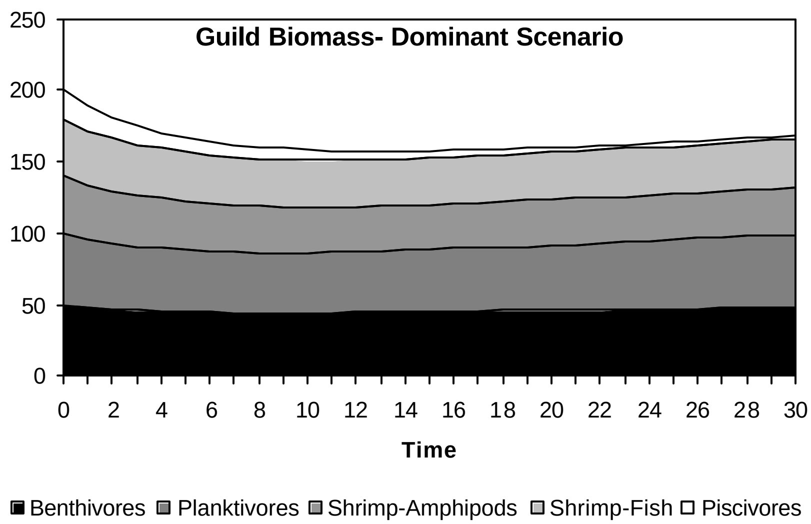


Figure 10. The results of the final scenario of the model, overfishing the dominant species in each guild.

A. Shows biomass among the various guilds. B. Shows biomass allocated to demersals and pelagics.



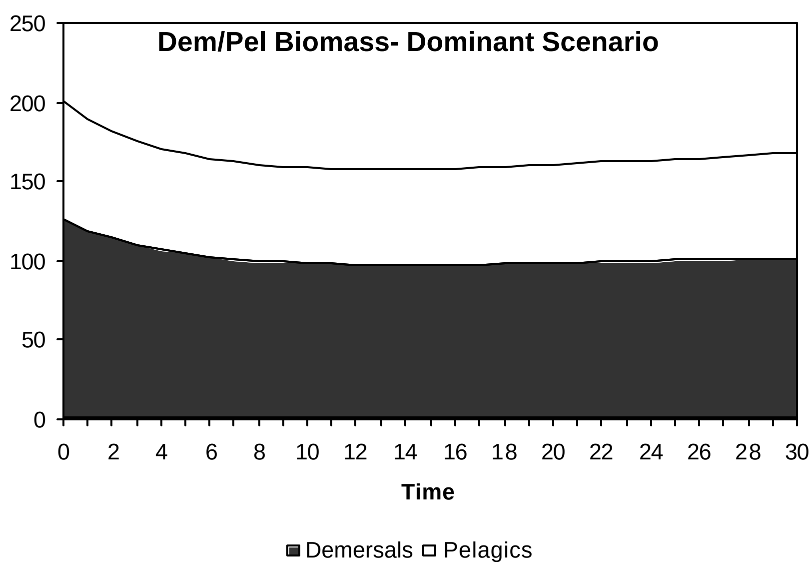


Figure 11. Single species trajectory for each member of a guild under the overfishing the dominant species in each guild scenario. A. Benthivores. B. Planktivores. C. Shrimp-amphipod feeders. D. Shrimp-fish feeders. E. Piscivores.