Estimation of demersal and pelagic species biomasses in the northeast USA continental shelf ecosystem

Jon K. T. Brodziak, Christopher M. Legault, Laurel A. Col and William J. Overholtz

Trophic models can quantify the constraints on production within an ecosystem. Such models require estimates of biomass across the spectrum of species assemblages, along with detailed knowledge of trophic interactions. In order to construct a food web model for the northeast USA continental shelf ecosystem, we estimated time series of demersal and pelagic species biomasses for four areas (Mid-Atlantic Bight, Southern New England, Georges Bank, Gulf of Maine) using spring and autumn research survey data. Species were grouped based on food habits and taxonomic relationships. Survey catchabilities were assumed to be similar within each group. We used a Bayesian estimation framework to characterize uncertainty in our results. An informative prior distribution for survey catchability was derived from published studies. Observed survey catchability data were taken from published studies and derived from stock assessments of individual species. Our results showed that total demersal and pelagic species biomass differed among regions, ranging from 29 $g \cdot m^{-2}$ in the Mid-Atlantic Bight to 16 $g \cdot m^{-2}$ in the Gulf of Maine. It was also evident that dramatic changes have occurred in the biomasses of major demersal and pelagic species groups across areas. There was a system-wide increase in the abundance of commercial pelagic finfishes in the mid-1980s. Determining whether pelagic forage species will decrease if demersal predator abundance increases will be important for implementing an ecosystem approach to fisheries management in this region.

Keywords: ecosystem, model, survey catchability, Bayesian estimation, pelagic and demersal biomass

Jon K. T. Brodziak, Christopher M. Legault, Laurel A. Col and William J. Overholtz: NOAA Fisheries, Northeast Fisheries Science Center, Woods Hole Laboratory, 166 Water Street, Woods Hole, Massachusetts, 02543-1097, USA
[tel: +1 508 495 2365, fax: +1 508 495 2393, e-mail: Jon.Brodziak@NOAA.GOV]

1

Introduction

Trophic models can quantify the constraints on production within an ecosystem. Trophic interactions are complex in marine ecosystems (Link 1999). Knowledge of all food web interactions is not possible. As a result, approximation of energy flows is necessary for constructing trophic models. Trophic models also require estimates of standing stock across species assemblages. Such estimates are often difficult to obtain in practice due to a lack of assessment data for unexploited species. To address this need, we developed a Bayesian estimation approach to construct time series of groups of demersal and pelagic species biomasses in the northeast USA continental shelf ecosystem.

Research survey data form the basis of our approach for estimating the standing crop of demersal and pelagic species biomasses. The northeast USA continental shelf ecosystem has been monitored with regular standardized trawl surveys during both spring and autumn since 1968. We used the trawl survey data to estimate the relative biomasses of demersal and pelagic species groups, which were formed based on similarities in food habits and taxonomy. Relative biomass estimates were constructed for 4 subregions: the Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight. Relative biomass estimates were rescaled to absolute values using Bayesian estimates of survey catchability. In this context, we used informative prior distributions for survey catchability based on published studies. Posterior distributions of survey catchability were calculated using the informative priors and observed survey catchability data derived from published studies and recent stock assessments.

We assessed whether there were general patterns among the trends of demersal and pelagic biomasses across the four subregions. Correlations of demersal and pelagic species biomasses were examined to identify patterns of constraint or dominance among particular groups. Biomass estimates were also contrasted with water temperature anomalies and fishing effort to see if oceanographic conditions or harvest had any obvious associations with observed changes.

Materials and Methods

Survey data
Annual research survey data were collected from 1968-2003 to estimate demersal and pelagic biomasses using a stratified random sampling design (Azarovitz 1981). The Northeast Fisheries Science Center (NEFSC) spring and autumn bottom trawl survey catch data were grouped into 4 geographic regions (Figure 1): the Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight. Together, these ecosystem regions span roughly 250,000 km^2 of inshore (<27 m) and offshore habitat (Table 1). Each species that was captured during one or more surveys was categorized as either demersal or non-demersal. Three groups of demersal species were formed based on feeding preferences described in Collette and Klein-MacPhee (2002). These were: benthivores, piscivores, and omnivores along with all others. The demersal benthivore group was composed of species that primarily feed on benthic prey. This group included gadiformes, elasmobranchs, pleuronectiformes, perciformes, scorpaeniformes, and other benthivores (Appendix, Table A1). The demersal piscivore group included species that

feed primarily on fishes. This group included gadiformes, elasmobranchs, and other piscivores (Appendix, Table A2). The unclassified demersals was a large group composed of omnivorous species that either fed opportunistically on both benthos and fish (Appendix, Table A3) or unclassified southern demersal species whose food habits were not reported in Collette and Klein-MacPhee (2002). The pelagic biomass consisted of pelagic or semi-pelagic species that are commonly captured on surveys north of 35° North (Figure 1). Rare deepwater species and uncommon tropical migratory species were excluded since their contribution to overall pelagic biomass was very low. Three groups of pelagic species were formed based on their contribution to regional fisheries (Appendix 1). The commercial finfish group consisted of Atlantic herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and butterfish (*Peprilus triacanthus*). The squid group consisted of northern shortfin (*Illex illecebrosus*) and inshore longfin (*Loligo pealeii*) squids and unclassified cephalopods. The remaining group of other pelagics consisted of anadromous and meso-pelagic species along with sand lance (*Ammodytes americanus*) and the remaining unclassified pelagic species.

Survey catchability

Research survey catchability varies among species and groups of species. If it were known for a given species or group, survey catchability (Q) would provide a direct estimate of absolute biomass (B) based on the survey index value (I).

(1) $$B = \frac{I}{Q}$$

We assumed that the average survey catchability for each demersal or pelagic species group was constant and estimable. Seasonal estimates of average survey catchability were made for each species group during spring and autumn using the Bayesian estimation approach described below. The seasonal estimates of Q were then applied to spring and autumn survey swept-area biomass indices during 1968-2003 to produce an estimate of absolute biomass for each species group and season using (1). The seasonal estimates of absolute biomass were then averaged to produce an estimate of average annual biomass for each species group during 1968-2003.

Bayesian estimation approach

A priori, it was recognized that there were few direct observations to estimate the average catchability of many species groups. Given this lack of information, we chose to use a Bayesian estimation approach to incorporate prior information on catchability from previous studies. This enabled us to use both prior information and observed data to estimate seasonal catchabilities for species groups. A probability model (likelihood) was developed for observed catchability data where both model parameters and observed data were assumed to be random variables. The joint probability distribution for model-based catchability estimate (Q) and catchability data (D), denoted by p(Q, D), depended on the prior distribution of model parameters (see Informative priors below), denoted by p(Q) , and the likelihood of observing the data (see Likelihood of catchability observations below), denoted by $p(D \mid Q) \equiv L(D \mid Q)$.

(2) $$p(Q, D) = p(Q)p(D|Q)$$

Applying Bayes' rule for the conditional probability of model parameters given the data, the posterior distribution of model parameters was p(Q | D)

(3) $$p(Q|D) = \frac{p(Q, D)}{p(D)} = \frac{p(Q)p(D|Q)}{p(D)}$$

where the integrated likelihood p(D) was the constant

(4) $$p(D) = \int p(Q)p(D|Q)dQ$$

Since p(D) was constant with respect to the model parameters (which have been integrated out of the expression), the posterior distribution of model parameters is proportional to the product of the (informative) prior and the likelihood

(5) $$p(Q|D) \propto p(Q)p(D|Q)$$

Markov Chain Monte Carlo (MCMC) simulation (Gilks et al. 1996) was applied to numerically generate posterior samples from (5). MCMC simulates a random walk through the set of possible catchability values that converges to a stationary distribution that is exactly the posterior distribution of Q. This simulation was equivalent to numerically integrating (3). We used the WINBUGS 1.4 software for performing the MCMC calculations (Spiegelhalter et al. 2003). For each species group, two simulated chains of length 110,000 posterior samples of Q were generated. In the first chain the coefficient of variation (CV) for Q was 50% while CV[Q] = 75% in the second chain. The first 10,000 samples of both chains were discarded to burn them in (i.e., to eliminate dependence on the initial value of Q). Of the remaining 100,000 samples in each chain, every other sample was discarded to eliminate the possibility of autocorrelation. This left 100,000 posterior samples of Q, 50,000 from each chain, for inference. Inferences about the estimated absolute biomasses of species groups were based on this numerical integration of p(Q | D). For example, the expected value of biomass of the jth species group (B_j) in a given year was calculated from N=100,000 posterior samples of the survey catchability of the jth species group ($Q^1, Q^2, Q^3, ...$) as

(6) $$E\left[B_j \mid D\right] \approx \frac{1}{N}\sum_{T=1}^{N} B_j\left(Q^T\right)$$

<u>Informative priors</u>

Prior information on NEFSC research survey catchabilities were available from two sources: Edwards (1968) and Clark and Brown (1977). In the former study, Edwards developed estimates of NEFSC survey catchability for 27 species based on their seasonal availability within the survey region and their vulnerability to the survey trawl gear. These survey catchability estimates were scaled to adjust survey swept-area biomass indices to absolute biomasses. In Clark and Brown's study, estimates of NEFSC autumn survey catchability were developed for

several species using estimates of fishing mortality, total catch and stock size, and relative survey abundance indices. These catchability estimates were appropriate for scaling survey mean catch biomass per tow and were rescaled to swept-area values for comparison with Edwards' results.

The informative prior for catchabilities of both demersal and pelagic species groups was assumed to be a gamma distribution with shape (r) and scale (μ) parameters.

(7) $$p(Q|r,\mu) \sim Gamma(r,\mu) = \mu^r Q^{r-1} \frac{e^{-\mu Q}}{\Gamma(r)} \quad for \, Q > 0$$

This choice provided a flexible positive distribution with mean equal to $E[Q] = r/\mu$ and coefficient of variation equal to $CV[Q] = r^{-0.5}$.

For the demersal species groups, the expected value of the informative catchability prior was determined from Edwards (1968) catchability estimate for "All others" species group (Q=0.16) and Clark and Brown's (1977) untransformed catchability estimate for "Other finfish" (Q=0.13, CV=31%). These two values were chosen because they represented general groups of species that were not actively targeted by commercial fisheries at that time. We set the expected value of the catchability prior to equal the average of the two catchability estimates so that E[Q] = 0.145. Given the expected value of Q, the CV[Q] was assumed to be 50%. This implied that the informative prior was more variable than Clark and Brown's estimate of survey Q.

The shape and scale parameters of the informative prior for demersal species groups were also parameters in the estimation model. Both were assumed to be distributed as a gamma random variable with parameters chosen to match the values of E[Q] and CV[Q]. In particular, the hyperprior for the shape parameter r was distributed as Gamma(16, 4). This implied that the expected value of r was E[r] = 4 with CV[r]=25%. The hyperprior for the scale parameter μ was distributed as Gamma(16, 0.58). This implied that the expected value of μ was E[μ] = 27.6 with CV[μ]=25%. These choices led to E[r]/E[μ] = E[Q] = 0.145 and CV[Q] = 50%.

For the pelagic species groups, there were relatively few catchability observations. As a result, informative priors were developed for individual species or groups although results were summarized using the pelagic species groups described above. There were also some more recent data on the likely values of pelagic survey catchabilities in Harley et al. (2001). Although Harley et al.'s study was not based on NEFSC survey data, we assumed that their estimates of trawl survey catchabilities were similar enough to provide adequate priors for Q in the absence of other information.

The expected values of the informative priors for pelagics were set using published values in Edwards (1968) and Harley et al. (2001). Field experience and judgment were used to identify species with similar behaviors and catchabilities. The coefficient of variation of Q was set to be 50% for all species and groups. The informative prior for Atlantic herring and mackerel had an expected catchability of E[Q] = 0.014 based on the average of the Qs for Atlantic herring and argentine (*Argentina silus*) reported in Harley et al. (2001). The expected value for butterfish

was E[Q] = 0.17 based on the average of the Qs for butterfish and Acadian redfish (*Sebastes fasciatus*) reported in Edwards (1968). The expected survey catchability for the unclassified pelagics excluding sand lance, squid, and mesopelagics groups was E[Q] = 0.08. This was the average of Qs for Atlantic herring and argentine from Harley et al. (2001) and butterfish and alewife (*Alosa pseudoharengus*) from Edwards (1968). The expected value for sand lance was E[Q] = 0.0009 from Harley et al. (2001). Last, the expected value for the anadromous group was E[Q] = 0.22 based on the value for alewife in Edwards (1968). For each of the individual pelagic species or groups, the hyperprior for the shape parameter was distributed as a Gamma(16, 4) random variable with an implied CV[r]=50%. Similarly, the hyperprior for the scale parameter was distributed as Gamma(16, x) where the value of "x" was determined by E[μ] = E[r]/E[Q].

Observed catchability data

There were two sources of survey catchability observations (Q^{OBS}) for the demersal species groups: Edwards (1968) and catchability observations derived from stock assessment data. Edwards (1968) provided survey catchability data for a total of 23 species (Table 2). Of these, the same catchability data was used for benthivore and omnivore elasmobranchs given the similarity in their benthic habitats and body shapes. These catchabilities were used as average values for autumn and spring since Edwards included seasonal availability as a factor in their calculation. There were a total of 12 catchability observations derived from assessment data (Table 2). All of these were derived from age-structured assessment information (NEFSC 2002, NEFSC 2003a, NEFSC 2003b, Terceiro 2003), with the exception of spiny dogfish (*Squalus acanthias*, NEFSC 2003b). Separate catchability values for autumn and spring were derived by regressing survey swept-area biomass (thousand mt) on stock biomass (thousand mt) over the assessment time period. The slopes of these regressions were the observed survey catchabilities. This approach was used for 11 stocks. Seasonal differences in catchability were apparent for some stocks, for example American plaice (*Hippoglossoides platessoides*), but not others. For spiny dogfish, the assessment-based catchability was derived as the ratio of total spring survey swept-area biomass during 1990-2002 to total biomass estimated using the minimum trawl herding assumption (NEFSC 2003b, Tables B6.2 and B7.3) during the same period.

Pelagic survey catchability observations for the commercial finfish species group were derived from recent assessments of Atlantic herring (Overholtz et al. 2004), mackerel (NEFSC 2000), and butterfish (NEFSC 2004). As with the demersal species assessment data, catchability values for autumn and spring were derived by regressing survey swept-area biomass on stock biomass over the assessment time period. The slopes of the regressions gave the observed survey catchability values for the pelagic commercial finfish group (Table 2).

Likelihood of catchability observations

The likelihood of a single catchability observation was a gamma distribution (eqn 3) with shape and scale parameters set by the informative priors. Seven demersal subgroups did not have any catchability observations (Table 2). These were: other benthivores, other omnivores, and the five unclassified southern demersal species subgroups. For the pelagic groups, only the pelagic

commercial finfish group had catchability observations (Table 2). Catchabilities of the remaining groups that had no catchability observations were determined by their informative priors. The joint likelihood of a total of n catchability observations (Q_i) was

(8) $$L\left(D|\theta\right) = \left(\frac{\mu^r}{\Gamma(r)}\right)^n \prod_{i=1}^{n} Q_i^{r-1} e^{-\mu Q_i}$$

Average biomass production

Average biomass production per unit area was computed for each species group, region, and year. There were some obvious outliers due to variability in survey catches. These outliers had a disproportionate influence on average biomass. To identify outliers in an objective manner we computed biomass production anomalies (B^{ANOM}) for each group and region using the median ($B_{0.5}$) and standard deviation (σ_B) of the observed values (B^{OBS})

(9) $$B^{ANOM} = \frac{B_{0.5} - B^{OBS}}{\sigma_B}$$

We removed outliers based on the biomass production anomalies. For demersal species groups, an observed value was an outlier if $B^{ANOM} > 3$. The pelagic species groups had higher intrinsic catch variability in the bottom trawl survey data. For pelagic species groups, an observed value was an outlier if $B^{ANOM} > 4$. Applying this criterion led to removal of 10 outliers out of a total of 864 observed values ($\approx 1\%$).

Average biomass production per unit area (grams per square meter) was computed for each species group and region over the period 1968-2003. This was done to see if there were regional differences in biomass production by individual species groups. Average total biomass production for demersal and pelagic species groups was also computed along with the percent contribution of each group to the total. This was expected to show whether the production of demersal and pelagic biomass differed among regions. Last, the average total production of both demersal and pelagic biomass was computed for each region to determine differences in total biomass production among regions.

Patterns in biomass production

We evaluated whether there were obvious patterns of biomass production among species groups and regions using time series plots and correlation analyses. We examined time series plots of biomass estimates by species group and region to discern patterns in biomass production. Four correlation analyses were conducted to investigate potential associations among species groups. First, Pearson correlation coefficients between total demersal and pelagic biomass production across regions were calculated to see if production was coherent across regions. Second, correlation coefficients of total biomass production across regions were computed to see if trends in total production were similar. Third, we computed correlations between demersal and pelagic

7

species groups within regions to see if there were patterns within regions. Fourth, we evaluated correlations among individual species groups across regions to see if there were any patterns among the groups. In each analysis, a correlation with absolute value $|\rho| > 0.325$ was deemed to be important. This choice was based on the critical value for testing whether $\rho=0$ at the $\alpha=0.05$ significance level with 35 data points, roughly the number of values in each biomass time series.

We also investigated whether there was a linear association between changes in water temperature and biomass production using correlation analyses. Pearson correlation coefficients between demersal and pelagic species groups and bottom and surface water temperature anomalies computed using the methods of Mountain et al. (2004) were calculated for the period 1968-2003 (Figure 2). Correlations within and across regions were computed to see if there were regional or system-wide associations between temperature and production. As described above, correlations with $|\rho| > 0.325$ were judged to be important.

Fishing effort is often thought to have an important impact on biomass production by direct removal of biomass through harvest. To evaluate the impacts of changes in fishing effort, we used a time series of standardized demersal and standardized total demersal and pelagic fishing effort on Georges Bank during 1968-1987 taken from Mayo et al. (1992). A nonparametric measure of association that was robust to departures from normality and potential outliers was used to compare effort and biomass. In particular, Spearman's coefficient of rank correlations (R) were calculated between standardized demersal fishing effort and the time series of total biomass production on Georges Bank for demersal species groups. Spearman correlations between total effort and total biomasses of Georges Bank demersal and pelagic species groups as well as overall total biomass were also calculated. We tested whether $R>0$ at the $\alpha=0.05$ significance level for all pairwise comparisons of fishing effort and biomass production. A one-sided test was used since the primary question was whether fishing effort had a positive or a negative association with biomass production.

Results

Average biomass production

Total demersal biomass production differed among regions (Table 3). On average, Georges Bank had the highest demersal biomass (14 g·m^{-2}) while the Gulf of Maine had the lowest (10 g·m^{-2}). The Mid-Atlantic Bight had the most variability in demersal biomass and the Gulf of Maine had the least variability. Overall, total demersal biomass was less variable than biomass for the individual demersal groups.

Biomass production by the individual demersal groups also differed among regions (Table 3). The highest average benthivore biomass was in the Mid-Atlantic Bight (5 g·m^{-2}) while the lowest was in Southern New England (2 g·m^{-2}). Average piscivore biomass ranged from a low of 6 g·m^{-2} in the Mid-Atlantic Bight and Georges Bank to a high of 8 g·m^{-2} in Southern New England. The highest average omnivore biomass was on Georges Bank (5 g·m^{-2}). In comparison, omnivore biomass was only 1 g·m^{-2} in the Gulf of Maine and the Mid-Atlantic.

Benthivore biomass varied substantially in each region with CVs ranging from 35-50%. Piscivore and omnivore biomasses were also highly variable with CVs of 40-65%. The exception was the Gulf of Maine piscivore biomass which was the least variable of all the groups (CV=23%).

Individual demersal groups contributed differing percentages to the total demersal biomass by region (Table 3). The piscivore group was the dominant group in each region. Its contribution to total demersal biomass ranged from a low of 37% for Georges Bank to a high of over 60% in the Gulf of Maine and Southern New England. The benthivore group was the 2nd dominant group in the Gulf of Maine (31%) and Mid-Atlantic Bight (41%). These regions also had the lowest percent composition of omnivores (9%). In comparison, the omnivore group was 2nd dominant on Georges Bank (34%) and in Southern New England (20%).

Total pelagic biomass averages differed among regions (Table 4). The highest pelagic biomass was in the Mid-Atlantic Bight (17 g·m^{-2}) and the lowest was in the Gulf of Maine (6 g·m^{-2}). The variability of total pelagic biomass was greater than demersal biomass with CVs ranging from 73-148%. Georges Bank and Southern New England were the most similar in terms of average pelagic biomass and its variability.

Average biomasses of pelagic groups also differed among regions (Table 4). Biomass of the commercial pelagic group was highest in Southern New England (7 g·m^{-2}) and was 3-fold lower in the Gulf of Maine (2 g·m^{-2}). The other pelagics group biomass was about 12 g·m^{-2} in the Mid-Atlantic Bight but averaged only 4 g·m^{-2} in the other regions. Squid biomass was generally lower than the other two groups. Biomass of squid was highest in Southern New England (3 g·m^{-2}) and about 10-fold lower in the Gulf of Maine (0.2 g·m^{-2}). Variability of the individual pelagic groups was generally much greater than for the demersal groups with CVs of over 100% in half of the pelagic groups. The least variable group was the squid group while the other pelagics group was the most variable.

The percent composition of total pelagic biomass was more similar across regions than the composition of demersal biomass (Tables 3 and 4). The commercial pelagics group was dominant in each region, except the Mid-Atlantic Bight. The commercial pelagics contributed about 50% of total pelagic biomass in the Gulf of Maine, Georges Bank, and Southern New England and about 40% in the Mid-Atlantic Bight. The other pelagics group was dominant in the Mid-Atlantic Bight (42%) and was 2nd dominant on Georges Bank and the Gulf of Maine (36-37%). The squid group was 2nd dominant in Southern New England (26%) but was the least abundant group in the other three regions.

The average percent composition of demersal and pelagic total biomass exhibited a north to south gradient (Table 5). The Gulf of Maine had the highest percentage of demersal biomass (74%) while the Mid-Atlantic Bight had the lowest demersal percentage (48%). Both Southern New England and the Mid-Atlantic Bight had roughly equal percentages of demersal and pelagic total biomass. In contrast, the Gulf of Maine had roughly 3-fold more demersal than pelagic biomass while Georges Bank had 2-fold more demersal biomass. The average percentage of

demersal biomass by region was less variable than pelagic biomass, except for the Mid-Atlantic Bight. In particular, the Gulf of Maine had the most variable average percentage of pelagic biomass (CV=85%).

Total biomass production also exhibited a north to south gradient (Table 5). Average total biomass production was highest in the Mid-Atlantic Bight (29 g·m^{-2}) and lowest in the Gulf of Maine (16 g·m^{-2}). Average total biomass was about 24 g·m^{-2} on Georges Bank and in Southern New England. These two regions also had the least variability in average total biomass (CVs of 34-38%). In comparison, variability in average total biomass was almost 2-fold greater in the Gulf of Maine and Mid-Atlantic Bight.

Patterns in biomass production

Patterns in biomass production differed among demersal species groups (Figure 3). Biomasses of the demersal benthivores increased across regions in the mid1970s. This group was at a relatively low abundance across regions in the 1980s. Since 1995, there has been an increase in demersal benthivore biomass across regions. Overall, demersal benthivore biomasses exhibited similar trends across regions.

In contrast, biomass trends for the demersal piscivores differed among regions (Figure 3). Piscivore biomass increased in the Gulf of Maine and Georges Bank in the 1960s-mid-1970s, then fluctuated without trend in the Gulf of Maine and gradually decreased on Georges Bank. Piscivore biomasses in Southern New England and the Mid-Atlantic Bight exhibited more variability. Piscivore biomass was relatively high in the early-1990s in Southern New England and has been lower since then. In contrast, piscivore biomass in the Mid-Atlantic Bight increased during 1985-1995, dropped sharply, and then increased again during the late-1990s.

Biomass patterns for the unclassified demersal group also differed among regions (Figure 3). There was a long-term decline in unclassified biomass in the Gulf of Maine. In contrast, there was an increase in unclassified biomass on Georges Bank until around 1980 when biomass declined then stabilized in the early-1990s. Unclassified demersal biomass increased in Southern New England until the early-1990s. Biomass subsequently declined for a few years then increased again the late-1990s. Biomass of unclassified demersals in the Mid-Atlantic Bight increased in the early-1970s and then remained relatively constant until the late-1990s when it again increased.

Patterns in pelagic biomass production also differed among species groups (Figure 4). Abundances of the commercial pelagics group were low in all regions until the mid-1980s. Commercial biomasses then increased across regions and have remained relatively high. Overall, the commercial pelagics exhibited similar biomass patterns across regions.

Biomass production of squids also exhibited similar patterns across regions (Figure 4). In the early-1970s squid biomass increased in all four regions. Squid biomass declined to a lower abundance in the early-1980s across all regions except Southern New England and has fluctuated

without trend since then.

Other pelagics also showed relatively similar patterns in biomass production across regions (Figure 4). Biomass of the other pelagics group was relatively low until the mid- to late-1970s when it increased substantially across regions. Abundances of other pelagics subsequently declined across regions in the early-1980s and has fluctuated without trend since then.

There were some similar patterns among the demersal and pelagic groups. Many of the demersal groups exhibited an increase in biomass during some part of the 1970s and again had an increasing trend in the late-1990s (Figure 3). However, the demersal benthivores was the only group that exhibited similar biomass patterns across regions. For the pelagic groups, patterns in biomass production were consistent across regions for each group (Figure 4). Biomass of he pelagic commercial finfish group was low until the mid-1980s when abundance increased in each region. Similarly, the biomass of squids increased in the early-1970s across regions, subsequently decreased, and fluctuated without trend since the early-1980s. The other pelagics also had a consistent pattern of low-high-low abundance across regions. Overall, biomass patterns of the pelagic groups changed in a similar manner across regions although the patterns differed among groups.

Similarities in time series of regional total demersal biomass and pelagic commercial finfish biomasses were also apparent (Figure 5). In the Gulf of Maine, total demersal biomass was over 10 $g \cdot m^{-2}$ from the late-1960 to early-1980s. Demersal biomass then declined and remained low until the late-1990s when it again increased above 10 $g \cdot m^{-2}$. In comparison, pelagic commercial biomass in the Gulf of Maine was very low (< 1 $g \cdot m^{-2}$) until the mid-1980s when it began to increase steadily to above 2 $g \cdot m^{-2}$ in the late-1990s. On Georges Bank, total demersal biomass increased from about 10 $g \cdot m^{-2}$ in the early-1970s to over 20 $g \cdot m^{-2}$ in the mid-1980s. Demersal biomass subsequently declined to less than 10 $g \cdot m^{-2}$ in 1994, and since then, has increased to roughly its long-term average. In contrast, pelagic commercial biomass on Georges Bank was low and below average until the early-1990s when it increased to over 5 $g \cdot m^{-2}$. Total demersal biomass in Southern New England fluctuated about its long-term average until the late-1980s when it increased to over 15 $g \cdot m^{-2}$. It subsequently decreased to below 10 $g \cdot m^{-2}$ in the early-1990s and then increased in the mid-1990s to fluctuate about its long-term average. Pelagic commercial biomass in Southern New England was at or below average until the mid-1980s when it began to increase to well-above average since the early-1990s. Total demersal biomass in the Mid-Atlantic Bight was low in the early-1970s, fluctuated about its average during the mid-1970s to early-1990s, and had an increasing trend during the late-1990s. Overall, the patterns in total demersal biomass differed among regions. In contrast, pelagic commercial biomass showed a consistent increase across regions since the mid-1980s (Figure 5).

Total biomass production, the sum of total demersal and total pelagic biomasses, varied through time in each of the regions (Figure 6). In the northern part of the ecosystem, total biomasses in the Gulf of Maine and Georges Bank were low and roughly equal during the early-1970s. Total biomass in both regions increased substantially in the mid-1970s and subsequently declined in the early-1980s. Since then, total biomasses in both regions have increased. In contrast to the

11

early-1970s, total biomass of Georges Bank has been greater than in the Gulf of Maine since the early-1980s. Regardless, total biomasses in both regions were at or above average by the late-1990s. In the southern part of the ecosystem, total biomasses in Southern New England and the Mid-Atlantic Bight were below average in the early-1970s and increased in the late-1970s. Total biomass in the south subsequently decreased in the early-1980s. Since then, total biomass has fluctuated about its long-term average in both southern regions. Overall, total biomass in both northern and southern regions was below average in the early 1970s. Since the early-1980s, total biomass has increased in the north and fluctuated without trend in the south.

Correlation coefficients among total biomass series for demersal and pelagic groups across regions (GOM=Gulf of Maine, GB=Georges Bank, SNE=Southern New England, MAB=Mid-Atlantic Bight) were significant at the α=5% level in 5 out of 28 possible pairs (18%). This was about 3-fold more than expected due to chance alone. Two positive correlations between pelagic biomass were significant: GOM*SNE and GB*MAB. Three positive correlations between pelagic (P) and demersal biomass were significant: GB.D*MAB.P, GB.P*MAB.D, and SNE.P*MAB.D. This provided positive evidence that there were interrelationships between total demersal and total pelagic biomasses across regions.

Correlations between total biomass series across regions were significant for 2 out 6 possible pairs (33%) or about 6-fold more than expected. There were two significant positive correlations among total biomasses: GOM*SNE and GB* MAB. This also suggested that some associations existed among biomasses across regions.

Correlations among demersal (B=Benthivores, P=Piscivores, U=Unclassified) and pelagic (C=Commercial finfish, O=Other pelagics, S=Squid) species groups within regions suggested that different patterns of association existed within regions. In the Gulf of Maine, 2 of 12 possible correlations (13%) were significant. Of these, one was positive (GOM.P*GOM.S) and one was negative (GOM.U*GOM.C). This provided little evidence of associations among groups in the Gulf of Maine.

On Georges Bank, a total of 6 out of 15 correlations were significant (40%). There were 4 significant positive correlations between demersal and pelagic groups: GB.B*GB.O, GB.B*GB.S, GB.P*GB.O, and GB.P*GB.S. Two correlations were significant among demersal or pelagic groups: GB.P*GB.U and GB.O*GB.S. There were 8-fold more significant correlations than expected due to chance. This suggested that there were some associations among species groups on Georges Bank.

In Southern New England, there were 3 significant correlations among species groups (20%). Of these, two were negative (SNE.B*SNE.U and SNE.B*SNE.C) and one was positive (SNE.P*SNE.U). This provided some evidence of associations among species groups in Southern New England.

In the Mid-Atlantic Bight, a total of 3 out of 15 correlations were significant (20%). The three significant positive correlations were: MAB.B*MAB.U, MAB.P* MAB.U, and

MAB.B*MAB.C. Both the demersal benthivores and the unclassified demersals had two significant positive correlations. Overall, this suggested that there were some associations among demersal groups in the Mid-Atlantic Bight.

Correlations among individual species groups across regions showed that groups had different patterns of association across regions. For the demersal benthivore group, a total of 2 out of 6 correlations were significantly positive (33%). These were: GM.B*GB.B and GM.B*SNE.B. This suggested that the Gulf of Maine demersal benthivore group had a positive association with benthivores in neighboring regions. In contrast, the demersal piscivores had no significant correlations among regions, providing no evidence of association of piscivores across regions. The unclassified demersal group had a total of 4 out of 6 significant correlations (66%). Of these, two were positive (GB.U*SNE.U and SNE.U*MAB.U) and two were negative (GM.U*SNE.U and GM.U*MAB.U). This provided positive evidence that there were associations among the unclassified groups across regions. Overall, the unclassified species groups had the strongest evidence of association across regions among the three demersal species groups.

For each of the three pelagic species groups, 4 out of 6 possible correlations were significant (66%). All of the 12 significant correlations were positive. For the commercial finfish group, the significant correlations were: GM.C*GB.C, GM.C*SNE.C, GB.C*SNE.C, and SNE.C*MAB.C. The four signicant correlations for the other pelagics group were: GM.O*GB.O, GM.O*SNE.O, GB.O*SNE.O, and GB.O*MAB.O. For the pelagic squid group, the significant correlations were: GM.S*GB.S, GB.S*SNE.S, GB.S*MAB.S, and SNE.S*MAB.S. Overall, the number of positive correlations among pelagic species groups suggested that there were positive associations of groups across regions.

Correlations between species groups and bottom (BT) and surface (ST) water temperature within regions showed that temperature associations differed by region. In the Gulf of Maine, 1 out of 12 possible correlations were significant (8%). The single positive correlation was GM.P*GM.BT. This provided no evidence that temperature was associated with species group biomasses in the Gulf of Maine. On Georges Bank there were no significant correlations with temperature, again suggesting that temperature was not associated with species group biomasses. Similarly, in Southern New England there was only one significant positive correlation (SNE.U*SNE.ST). In contrast, 6 out of 12 significant positive correlations were detected in the Mid-Atlantic Bight: MAB.B*MAB.BT, MAB.B*MAB.ST, MAB.U*MAB.BT, MAB.U*MAB.ST, MAB.S*MAB.BT, and MAB.S*MAB.ST. This suggested that biomasses of demersal benthivores, unclassified demersals, and squids had a positive association with water temperature in the Mid-Atlantic Bight. Overall, it appeared that water temperature was likely associated with species group biomasses in the southernmost region of the northeast USA continental shelf ecosystem.

A significant negative Spearman rank correlation coefficient was detected between total fishing effort and total biomass ($R = -0.67$, $P < 0.01$) on Georges Bank. Spearman rank correlations were also significant for demersal ($R = -0.48$, $P = 0.02$) and pelagic ($R = -0.54$, $P = 0.01$) biomasses on Georges Bank (Figure 7). Similarly, a significant rank correlation was found between

demersal fishing effort and demersal biomass on Georges Bank (R = -0.44, P = 0.03). Correlations were also significant between demersal effort and demersal benthivore (R = -0.39, P = 0.05) and piscivore (R = -0.67, P = 0.03) biomasses, but not for unclassified demersals (R = -0.24, P = 0.15). Overall, these results suggested that high fishing effort was significantly associated with low demersal and pelagic biomass on Georges Bank.

Discussion

Differences in average total biomass across regions were consistent with differences in primary production. Average total biomass was lowest in the Gulf of Maine (16 g·m^{-2}) where annual primary production averages around 260-270 gC·m^{-2} (O'Reilly et al. 1987). In comparison, average total biomasses were about 50% higher in Southern New England and Georges Bank and 75% higher in the Mid-Atlantic Bight. Primary production in these regions ranges from 265-455 gC·m^{-2} on Georges Bank to 260-505 gC·m^{-2} in Southern New England and the Mid-Atlantic Bight (O'Reilly et al. 1987). The higher average total biomasses in the more productive regions is consistent with bottom-up forcing playing an important role in determining the standing crop of demersal and pelagic biomass in the northeast USA continental shelf ecosystem.

The north to south gradient in the percentage of total biomass contributed by demersal species is consistent with the average water temperature differences among the four regions. Although water temperature anomalies are generally coherent among regions (Figure 2), the Gulf of Maine tends to have cooler surface and bottom water temperatures throughout the year (Mountain and Holzwarth 1989). The deeper waters of this semi-enclosed basin provide a more stable year-round thermal regime than the continental shelf waters of Georges Bank, Southern New England, and the Mid-Atlantic Bight. Bottom temperatures in the Gulf of Maine range from roughly 5-8 °C year-round. In comparison, bottom temperatures in the more southerly regions range from 4-16 °C on Georges Bank and Southern New England to 5-20 °C in the Mid-Atlantic Bight. As a result, demersal habitat in the Gulf of Maine is more stable than in the continental shelf regions. In contrast, the two primary pelagic stocks, Atlantic herring and mackerel, are highly migratory planktivores that move south in winter to preferred water temperatures and north during summer in search of abundant food. The seasonal movements of these primary pelagics contribute to the higher variability in the percentage of pelagic species in both the Gulf of Maine and the Mid-Atlantic Bight.

The fact that we found differences in demersal and pelagic species groups abundances across regions is important for building a trophic model for the northeast USA continental shelf ecosystem. This finding implies that we need to incorporate regional spatial structure into the model. This will entail developing submodels for each region. These submodels will need to be linked through flows of energy between demersal and pelagic groups across regions, as suggested by the positive correlations among pelagic groups across regions. Regional differences in water temperatures reinforce this point since key vital rates, such as metabolism and the ratio of production to biomass, increase nonlinearly with increasing temperature (Brown et al. 2004).

The synchronous increase in demersal benthivore biomass across regions in the late-1990s was

coincident with fishery management actions to close large-scale areas in Southern New England, Georges Bank, and the Gulf of Maine to all bottom-tending fishing gears. Closed areas on Georges Bank and in Southern New England had a positive impact on rebuilding of Georges bank sea scallop, haddock, and yellowtail flounder stocks (Murawski et al. 2000). The fact that there was a system-wide increase is supported by the positive correlations among benthivore groups in Southern New England, Georges Bank, and the Gulf of Maine.

The synchronous increase in demersal piscivore biomass across regions in the mid- to late-1970s likely reflects increases due to reductions in fishing effort and mortality. In particular, spiny dogfish abundance generally increased during this period (NEFSC 2003). The negative correlation between piscivore abundance and fishing effort supports an inverse relation between the two. Changes in species dominance within the piscivore group may require separating out individual species for building a trophic model. For example, long-term increases in dogfish abundance on Georges Bank is thought to be due to the competitive release of food energy from overfished piscivorous groundfish, such as Atlantic cod, to spiny dogfish (Fogarty and Murawski 1998). Furthermore, Link and Garrison (2002) found that piscivore diets on Georges Bank tended to track prey abundance, but that total consumption was relatively constant. They also found that species dominance changed through time. The dominant piscivore was silver hake in the early-1970s, followed by Atlantic cod from the mid-1970s to 1985, and spiny dogfish from 1985 onwards. Thus, the composition of the piscivore species group on Georges Bank likely changed through time. In general, temporal changes in the composition of species groups need to be carefully considered when building trophic models. There is an implicit trade-off between gains in accuracy by estimating individual species abundance versus the gains in precision realized by evaluating abundances of species groups.

There was a system-wide increase in the abundance of commercial pelagic finfishes in the mid-1980s. This pattern is primarily due to the recovery of the Atlantic herring and mackerel stocks under light fishing pressure (Fogarty and Murawski 1998, Overholtz and Friedland 2002). The fact that these stocks increased across regions implies the need for considering fluxes between the primary pelagics across regions and species groups. This presents a challenge in matching the scales of the migratory and consumption processes when constructing a trophic model for the northeastern USA continental shelf ecosystem.

The fact that squid abundances were positively correlated among adjacent regions also suggested that fluxes among regions would be a relevant consideration for this species group. The general increase in squid abundance across regions in the early-1970s suggests a system-wide response by this species group. In this case, one possible mechanism could be increased water temperatures (Figure 2) which might have led to higher somatic growth rates (e.g., Brodziak and Macy 1996, Hatfield et al. 2001). This possibility is supported by the positive correlation between water temperatures and squid abundance in the Mid-Atlantic Bight. This may not be the case in other regions, however, since similar increasing trends in temperature during the 1990s do not appear to have had a similar positive effect (Figure 4). Alternatively, the squid increase during the early-1970s could have been due to predation release, as many of their finfish predators were fished to low abundances.

The system-wide increase in abundance of the other pelagics group in the late-1970s may also be due to trophic interactions. Much of the other pelagics increase was due to increased catches of sand lance. Fogarty et al. (1991) showed that the increase in sand lance recruitment could be explained by decreased abundances of Atlantic mackerel and herring which feed opportunistically on sand lance. The subsequent decline of other pelagics biomass in the mid-1980s across regions and continued low abundance through the 1990s is consistent with the hypothesis that sand lance recruitment may be regulated by herring and mackerel predation. The positive correlations among the other pelagics group across regions also provides empirical support for a common system-wide mechanism regulating the abundance of this group.

The inverse relationship between fishing effort and biomass on Georges Bank is consistent with the hypothesis that high fishing intensity reduces target and non-target species abundances. As total fishing effort dropped by 65% from an average of over 2.2 million hours fished per year (mhr·yr^{-1}) during 1968-1976 to less than 0.8 mhr·yr^{-1} during 1977-87, annual total biomass on Georges bank increased 68% from an average of 17 g·m^{-2} to 29 g·m^{-2}. The Georges Bank system has been severely perturbed by fishery impacts (Fogarty and Murawski 1998). Despite substantial changes in species composition and abundance, the use of large-scale closed areas on Georges Bank has improved abundances of some commercial species (Murawski et al. 2000) and may have helped to increase species richness as well (Brodziak and Link 2002). The continued use of closed areas combined with substantial cuts in fishing effort and trawl mesh size increases under Amendment 13 to the Northeast Multispecies Fishery Management Plan (NEFMC 2004) will provide an opportunity to see the ecosystem response to reduced fishery impacts.

It is also evident that substantial changes have occurred in the biomasses of major demersal and pelagic species groups across areas (Figures 3 and 4). The synchronous increase in pelagic relative to demersal biomass across regions in the 1990s (Figure 5) is consistent with a hypothesized shift in benthic versus pelagic energy fluxes within the ecosystem (Link 1999). If more energy flows through pelagic versus demersal species, the overall system energy efficiency might be expected to decrease for two reasons. First, if mean body mass declines as smaller-bodied pelagic species become numerically dominant, then average metabolic costs would be expected to increase (Brown et al. 2004) reducing system energy efficiency on a community-wide scale (see, for example, Choi et al. 2003). Second, empirical estimates of production to biomass (P/B) ratios indicate that the primary pelagics, herring and mackerel, have lower P/B ratios than dominant demersal species, such as cod, haddock, and yellowtail flounder (Sissenwine 1987). Overall, a shift in energy flux to smaller-bodied pelagics could restructure the northeast USA continental shelf ecosystem towards faster generation times and lower production efficiency. Such a restructuring has been described for the eastern Scotian Shelf ecosystem (Choi et al. 2003) where both over fishing and changing environmental conditions have been implicated as causal factors. In this context, the recent increases in some demersal species groups could reverse the apparent shift towards pelagic dominance through increased predation. Determining whether pelagic forage species will decrease if demersal predator abundance increases will be important for implementing an ecosystem approach to fisheries management in this region.

16

References

Azarovitz, T. R. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. *In* Bottom Trawl Surveys. Can. Spec. Sci. Pub. Fish. Aqua. Sci. 58:62-67.

Brodziak, J.K.T, and Macy, W.K., III..1996. Growth of long-finned squid, *Loligo pealei*, in the northwest Atlantic. Fish.Bull. 94:212-236.

Brodziak, J., and Link, J. 2002. Ecosystem-based fishery management: What is it and how can we do it? Bull. Mar. Sci. 70(2): 589-611.

Brown, J.H., Gillooly, J.F., Allen, A.P., and West, G.B. 2004. Towards a metabolic theory of ecology. Ecology 85(7):1771-1789.

Choi, J.S., Frank, K.T., Leggett, W.C., Drinkwater, K. 2004. Transition to an alternate state in a continental shelf ecosystem. Can. J. Fish. Aqua. Sci. 61:505-510.

Clark, S.H., and Brown, B.E. 1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel survey data. Fish. Bull. 75(1):1-21.

Collette, B.B, and Klein-MacPhee, G. [Eds.]. 2002. Bigelow and Schroeder's Fishes of the Gulf of Maine, 3rd Ed. Smithsonian Institution Press, Washington, D.C. 748 pp.

Edwards, R.L. 1968. Fishery resources of the North Atlantic area. *In* The future of the fishing industry of the United States. *Edited by* D.W. Gilbert. Univ. of Washington Publications in Fisheries, 4:52-60.

Fogarty, M.J., Cohen, E.B., Michaels, W.L., and Morse, W.W. 1991. Predation and the regulation of sand lance populations: an exploratory analysis. ICES mar. Sci. Symp. 193:120-124.

Fogarty, M.J., and Murawski, S.A. 1998. Large-scale disturbance and the structure of marine ecosystems: fishery impacts on Georges Bank. Ecol. Appl. 8(1) Suppl. pp. S6-S22.

Gilks, W.R., Richardson, S., and Spiegelhalter, D.G. [Eds.]. 1996. Markov chain monte carlo in practice. Chapman and Hall, London. 486 pp.

Harley, S.J., Myers, R., Barrowman, N., Bowen, K., and Admiro, R. 2001. Estimation of research trawl survey catchability for biomass reconstruction of the eastern Scotian Shelf. Canadian Science Advisory Secretariat. Res. Doc. 2001/084. 54 pp.

Hatfield, E.M.C., Hanlon, R.T., Forsythe, J.W., and Grist, E.P.M. 2001. Laboratory testing of a growth hypothesis for juvenile squid *Loligo pealeii* (Cephalopoda: Loliginidae). Can. J. Fish.

Aqua. Sci. 58:845-857.

Link, J. 1999. (Re)Constructing food webs and managing fisheries. *In* Ecosystem approaches for fisheries management. Univ. Of Alaska Sea Grant, AK-99-01, Fairbanks. pp. 571-588.

Link, J.S., and Garrison, L.P. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. Fish. Res. 55:71-86.

Mayo, R.K., Fogarty, M.J., and Serchuk, F.M. 1992. Aggregate fish biomass and yield on Georges Bank, 1960-87. J. Northw. Atl. Fish. Sci. 14:59-78.

Mountain, D.G., and Holzwarth, T.J. 1989. Surface and bottom temperature distribution for the northeast continental shelf. NOAA Tech. Mem. NMFS-F/NEC-73. 32 pp.

Mountain, D.G., Taylor, M.H., and Bascuñán, C. 2004 Revised Procedures for Calculating Regional Average Water Properties for Northeast Fisheries Science Center Cruises. NEFSC Ref. Doc. 04-08. Woods Hole, MA. 62 pp.

Murawski, S.A., Brown, R., Lai, H.-L., Rago, P.J., and Hendrickson, L. 2000. Large-scale closed areas as a fishery-management tool in temperate marine ecosystems: the Georges Bank experience. Bull. Mar. Sci. 66(3):775-798.

New England Fishery Management Council [NEFMC]. 2003. Final Amendment 13 to the Northeast Multispecies Fishery Management Plan including a Final Supplemental Environmental Impact Statement and an Initial Regulatory Flexibility Analysis. NEFMC, Newburyport, MA 01950, 1659 pp.
Available at: http://www.nefmc.org/nemulti/index.html

NEFSC [Northeast Fisheries Science Center]. 2000. Atlantic Mackerel. 30th Northeast Regional Stock Assessment Workshop (30th SAW). NEFSC Ref. Doc. 00-03. Woods Hole, MA. 37 pp.

NEFSC. 2002. Assessment of 20 northeast groundfish stocks through 2001. A report of the Groundfish Assessment Review Meeting. NEFSC Ref. Doc. 02-16. Woods Hole, MA. 478 pp.
NEFSC. 2003. 37th Northeast Regional Stock Assessment Workshop (37th SAW) Stock Assessment Review Committee (SARC) Consensus Summary of Assessments NEFSC Ref. Doc. 03-16. Woods Hole, MA. 603 pp.

NEFSC. 2004. Atlantic Butterfish. 38th Northeast Regional Stock Assessment Workshop (38th SAW). NEFSC Ref. Doc. 04-03. Woods Hole, MA. 72 pp.

O'Reilly, J., Evans-Zetlin, C. and Busch, D. 1987. Primary production. *In* Georges Bank *Edited by* R. Backus, R. Price, and D. Bourne. MIT Press, Cambridge, MA. pp. 220-233.

Overholtz, W.J., and Friedland, K.D. 2002. Recovery of the Gulf of Maine-Georges Bank

Atlantic herring (*Clupea harengus*) complex: perspectives based on bottom trawl survey data. Fish. Bull. 100:593-608.

Overholtz, W.J., Jacobson, L.D., Melvin, G.D., Cieri, M., Power, M.., Libby, D. and Clark, K.. 2004. Stock assessment of the Gulf of Maine-Georges Bank Atlantic herring complex, 2003. NEFSC Ref. Doc. 04-06. Woods Hole, MA. 290 pp.

Sissenwine, M.P. 1987. Fish and squid production. *In* Georges Bank *Edited by* R. Backus, R. Price, and D. Bourne. MIT Press, Cambridge, MA. pp. 347-350.

Spiegelhalter, D., Thomas, A., Best, N., and Lunn, D. 2003. WinBUGS User Manual. Available at: http://www.mrc.bsu.carn.ac.uk/bugs

Terceiro, M. 2003. Stock Assessment of Summer Flounder for 2003. NEFSC Ref. Doc. 03-09. Wood Hole, MA. 190 pp.

Wigley, S., Brodziak, J.K.T, and Col, L. 2003. Assessment of the Gulf of Maine and Georges Bank witch flounder stock for 2003. NEFSC Ref. Doc. 03-14. Woods Hole, MA. 194 pp.

Table 1. Total areas (km^2) of four regions (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) used to estimate demersal and pelagic biomasses in the northeast USA continental shelf ecosystem.

Region	Inshore	Offshore	Total	Percent
Gulf of Maine	8,949	61,368	70,317	29%
Georges Bank		52,478	52,478	21%
Southern New England	12,053	52,008	64,060	26%
Mid-Atlantic Bight	16,275	43,532	59,807	24%
Total	37,276	209,386	246,662	
Percent	15%	85%		

Table 2. Observed fall and spring trawl survey catchability values for demersal and pelagic groups based on Edwards (1968) or stock assessment data.

Group	Source	Species or stock	Fall value	Spring value
Benthivore gadiformes				
	Edwards	*Melanogrammus aeglefinus*	0.48	0.48
	Edwards	*Urophycis chuss*	0.07	0.07
	Assessment	Georges Bank haddock	0.33	0.38
Benthivore elasmobranchs				
	Edwards	*Dipturus laevis*	0.10	0.10
	Edwards	*Leucoraja ocellata*	0.20	0.20
	Edwards	*Leucoraja erinacea*	0.15	0.15
	Edwards	*Amblyraja radiata*	0.10	0.10
Benthivore pleuronectiformes				
	Edwards	*Hippoglossoides platessoides*	0.28	0.28
	Edwards	*Pseudopleuronectes americanus*	0.17	0.17
	Edwards	*Paralichthys oblongus*	0.49	0.49
	Edwards	*Glyptocephalus cynoglossus*	0.49	0.49
	Edwards	*Scophthalmus aquosus*	0.09	0.09
	Edwards	*Limanda ferruginea*	0.39	0.39
	Assessment	Cape Cod yellowtail flounder	0.14	0.14
	Assessment	American plaice	0.26	0.60
	Assessment	Gulf of Maine winter flounder	0.19	0.16
	Assessment	Witch flounder	0.09	0.09
	Assessment	Georges Bank yellowtail flounder	0.13	0.42
	Assessment	Southern New England yellowtail flounder	0.16	0.26
	Assessment	Southern New England winter flounder	0.17	0.18
Benthivore perciformes				
	Edwards	*Macrozoarces americanus*	0.31	0.31
	Edwards	*Stenotomus chrysops*	0.05	0.05
Benthivore scorpaeniformes				
	Edwards	*Myoxocephalus octodecemspinosus*	0.42	0.42
	Edwards	*Sebastes fasciatus*	0.27	0.27
	Edwards	*Hemitripterus americanus*	0.90	0.90
	Assessment	Redfish	0.34	0.36
Piscivore gadiformes				
	Edwards	*Gadus morhua*	0.28	0.28
	Edwards	*Pollachius virens*	0.08	0.08
	Edwards	*Merluccius bilinearis*	0.04	0.04
	Edwards	*Urophycis tenuis*	0.51	0.51
	Assessment	Gulf of Maine cod	0.30	0.27
	Assessment	Georges Bank cod	0.11	0.29
Piscivore elasmobranchs				
	Edwards	*Squalus acanthias*	0.29	0.29
	Assessment	Spiny dogfish	0.95	0.95
Piscivore other				
	Edwards	*Lophius americanus*	0.32	0.32
	Assessment	Fluke	0.04	0.06
Commercial pelagics				
	Assessment	Herring	0.02	0.11
	Assessment	Mackerel	0.04	0.04
	Assessment	Butterfish	0.21	0.89

Table 3. Average demersal species biomass (g·m^{-2}) and coefficient of variation (% in parentheses) during 1968-2003 by species group and region, along with average percent composition of total demersal biomass by species group within each region.

	Demersals (g·m^{-2})			
Region	Benthivores	Piscivores	Omnivores	Total
Gulf of Maine	3.3 (40%)	6.2 (23%)	0.9 (65%)	10.4 (21%)
Georges Bank	3.8 (35%)	5.6 (44%)	5.2 (50%)	14.4 (31%)
Southern New England	2.1 (41%)	7.7 (40%)	2.4 (43%)	12.0 (30%)
Mid-Atlantic Bight	4.5 (50%)	5.8 (51%)	1.0 (55%)	11.3 (40%)

	Demersal Percentage by Species Group		
Region	Benthivores	Piscivores	Omnivores
Gulf of Maine	31%	61%	9%
Georges Bank	28%	37%	34%
Southern New England	19%	61%	20%
Mid-Atlantic Bight	41%	50%	9%

Table 4. Average pelagic species biomass (g·m^{-2}) and coefficient of variation (% in parentheses) during 1968-2003 by species group and region, along with average percent composition of total pelagic biomass by species group within each region.

Region	Commercial finfish	Pelagics (g·m^{-2}) Other pelagics	Squids	Total
Gulf of Maine	1.9 (133%)	4.0 (234%)	0.2 (93%)	6.2 (148%)
Georges Bank	5.1 (125%)	3.9 (133%)	1.0 (76%)	10.1 (73%)
Southern New England	6.6 (86%)	3.9 (216%)	2.6 (39%)	13.3 (73%)
Mid-Atlantic Bight	4.4 (91%)	11.5 (195%)	1.7 (51%)	17.4 (125%)

Region	Pelagic Percentage by Species Group Commercial finfish	Other pelagics	Squids
Gulf of Maine	53%	36%	10%
Georges Bank	48%	37%	15%
Southern New England	54%	21%	26%
Mid-Atlantic Bight	38%	42%	20%

Table 5. Average percent composition of total biomass from demersal and pelagic total biomass by region and coefficient of variation (% in parentheses) along with total average biomass production (g·m^{-2}) by region and coefficient of variation (% in parentheses).

	Average Composition	
Region	Percent Demersal	Percent Pelagic
Gulf of Maine	74 (30%)	26 (85%)
Georges Bank	63 (27%)	37 (47%)
Southern New England	52 (28%)	48 (31%)
Mid-Atlantic Bight	48 (38%)	52 (36%)

Total Biomass	
Region	Total (g·m^{-2})
Gulf of Maine	16.4 (60%)
Georges Bank	24.3 (38%)
Southern New England	24.1 (34%)
Mid-Atlantic Bight	28.7 (77%)

Figure 1. Map showing four regions (Gulf of Maine [GOM], Georges Bank [GB], Southern New England [SNE], and the Mid-Atlantic Bight [MAB]) used to estimate demersal and pelagic biomasses in the northeast USA continental shelf ecosystem.
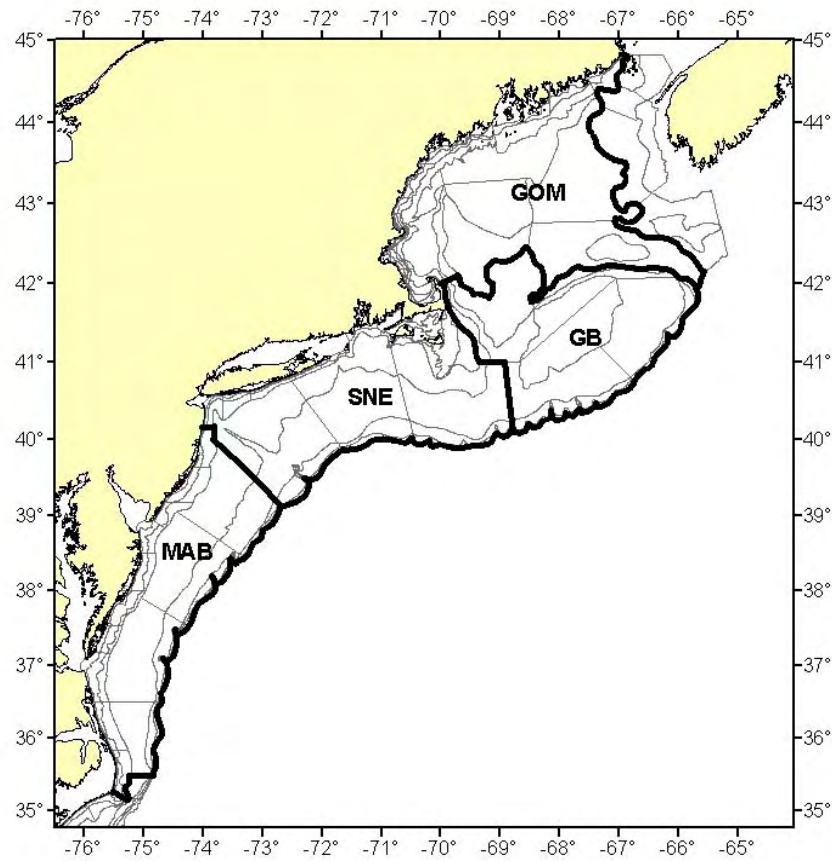
Figure 2. Time series of bottom and surface water temperature anomalies in four regions of the northeast USA continental shelf ecosystem (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) during 1968-2003.

Figure 3. Time series of annual demersal biomass production (g·m^{-2}) by benthivores, piscivores, and unclassified species in four regions of the northeast USA continental shelf ecosystem (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) during 1968-2003.
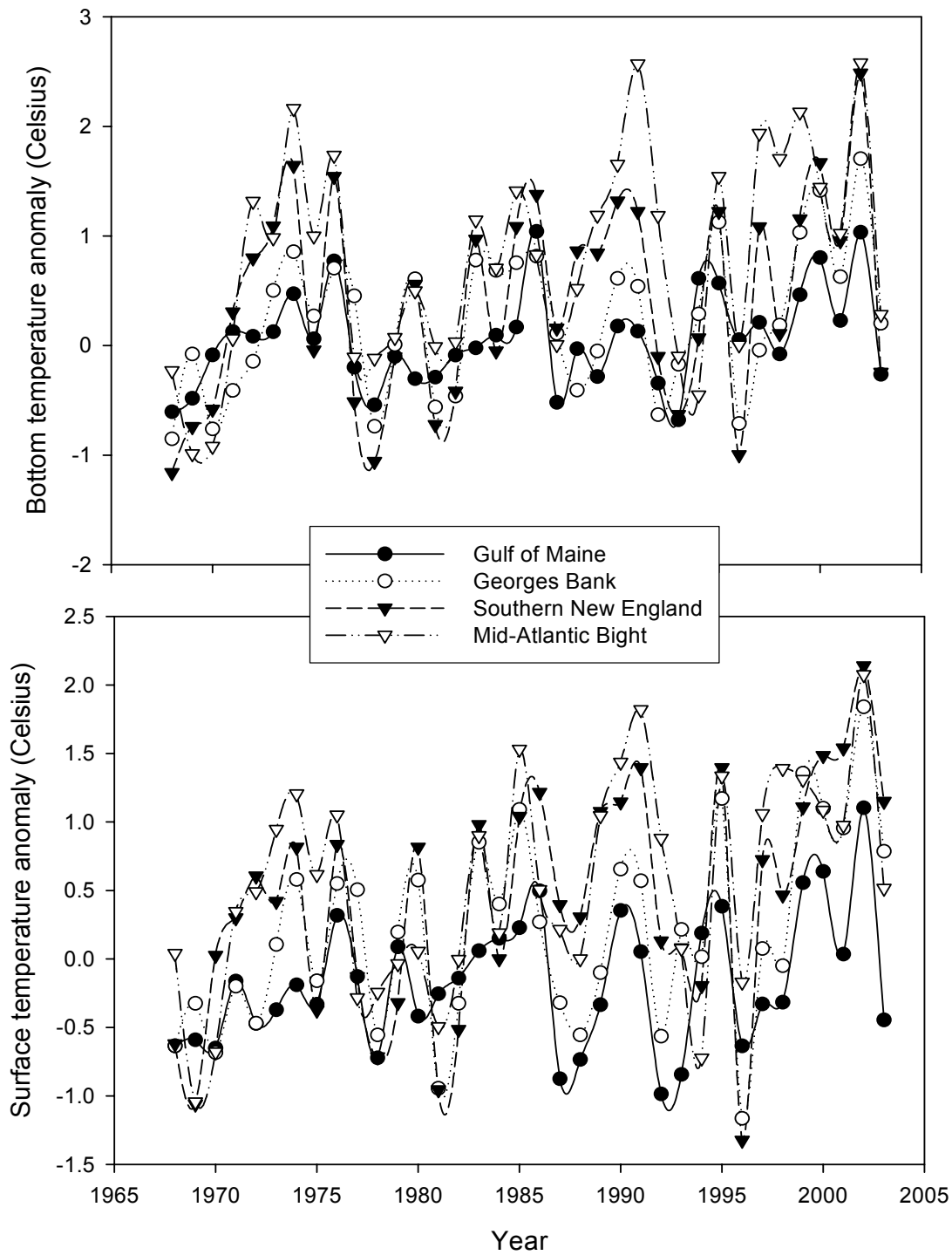
Figure 4. Time series of annual pelagic biomass production (g·m^{-2}) by pelagic commercial finfish, squid, and other pelagics species in four regions of the northeast USA continental shelf ecosystem (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) during 1968-2003.

Figure 5. Time series of total demersal and pelagic species biomasses (g·m^{-2}) in four regions of the northeast USA continental shelf ecosystem (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) during 1968-2003
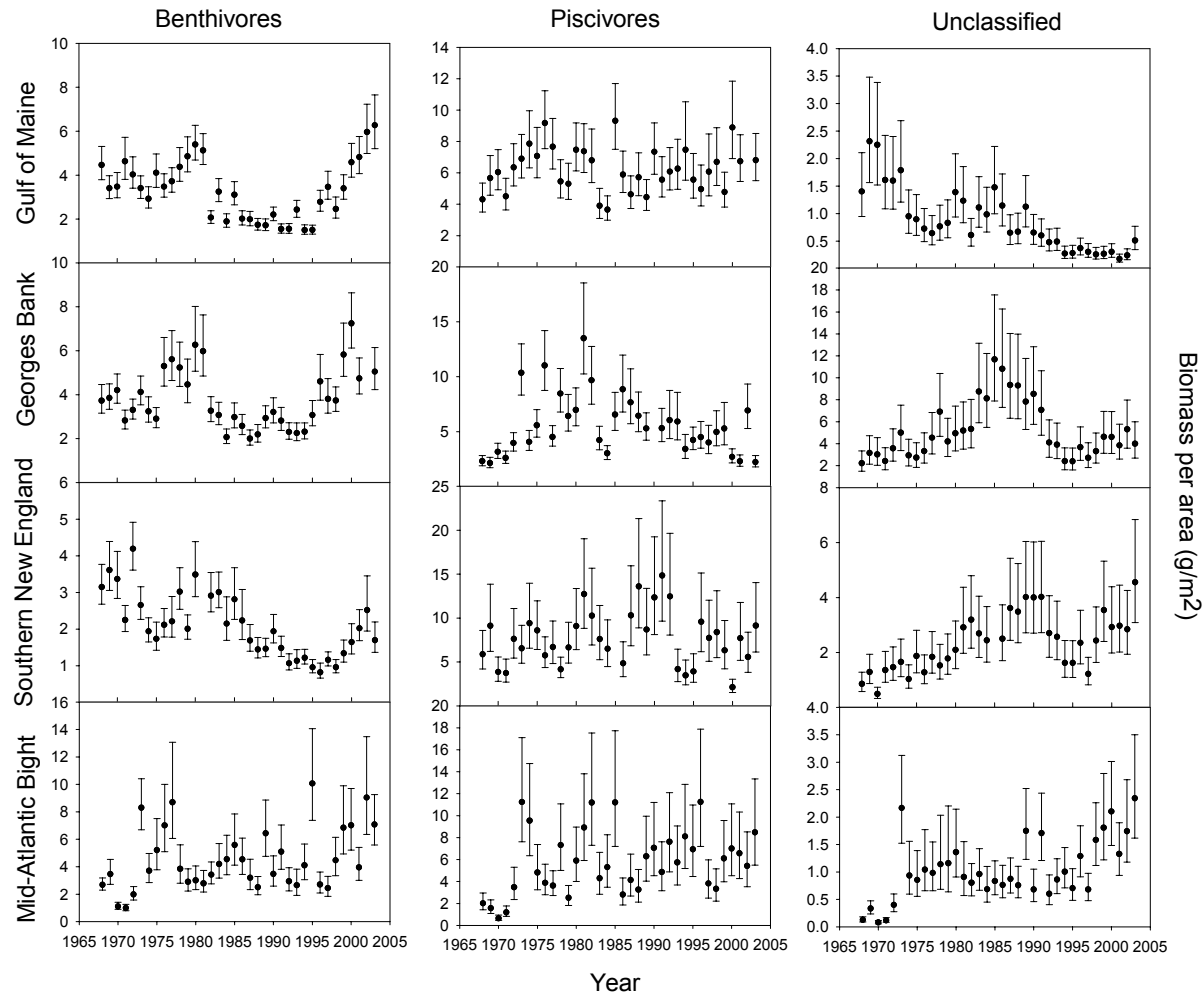
Figure 6. Time series of total demersal and pelagic biomass ($g \cdot m^{-2}$) in four regions of the northeast USA continental shelf ecosystem (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) during 1968-2003.
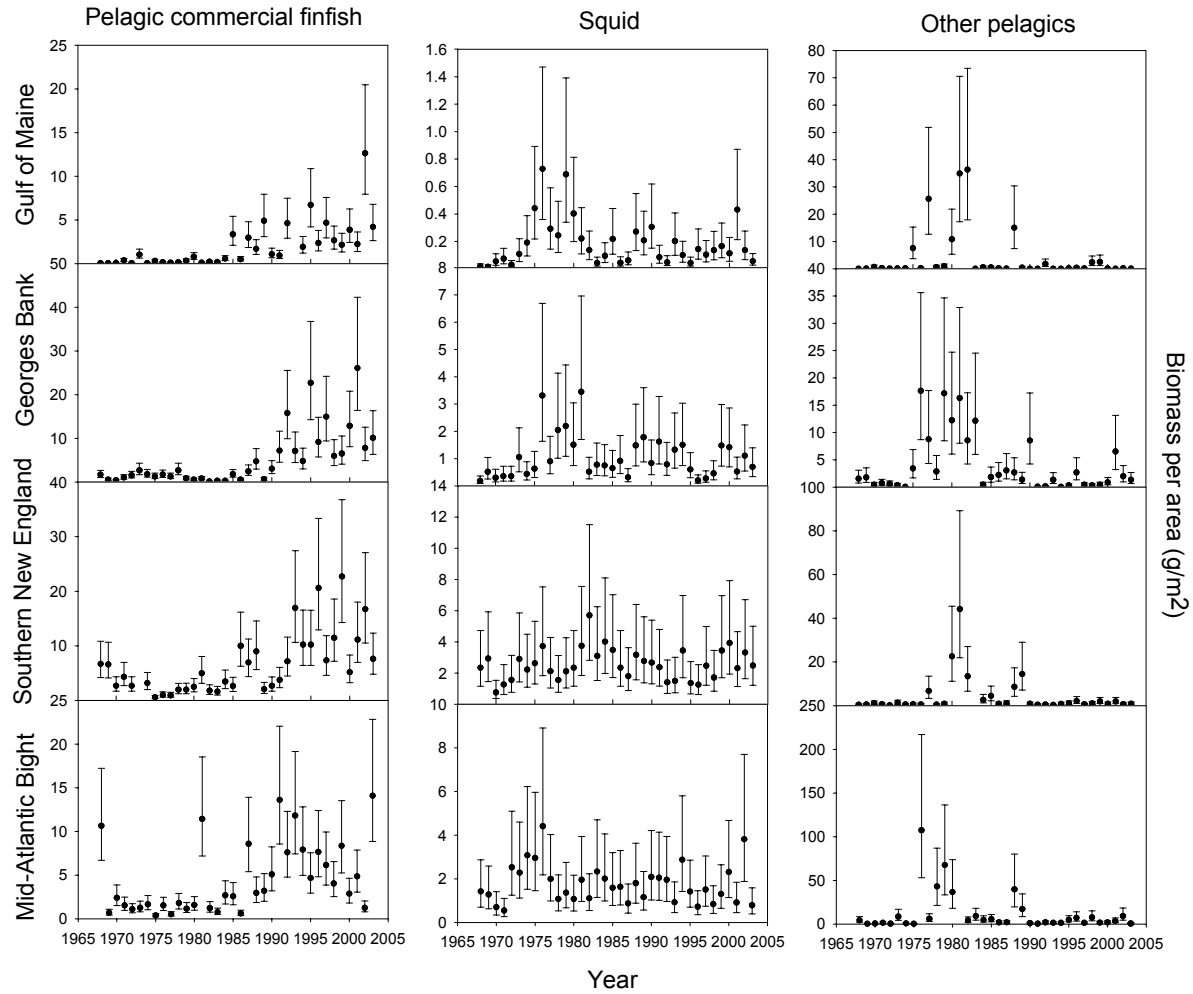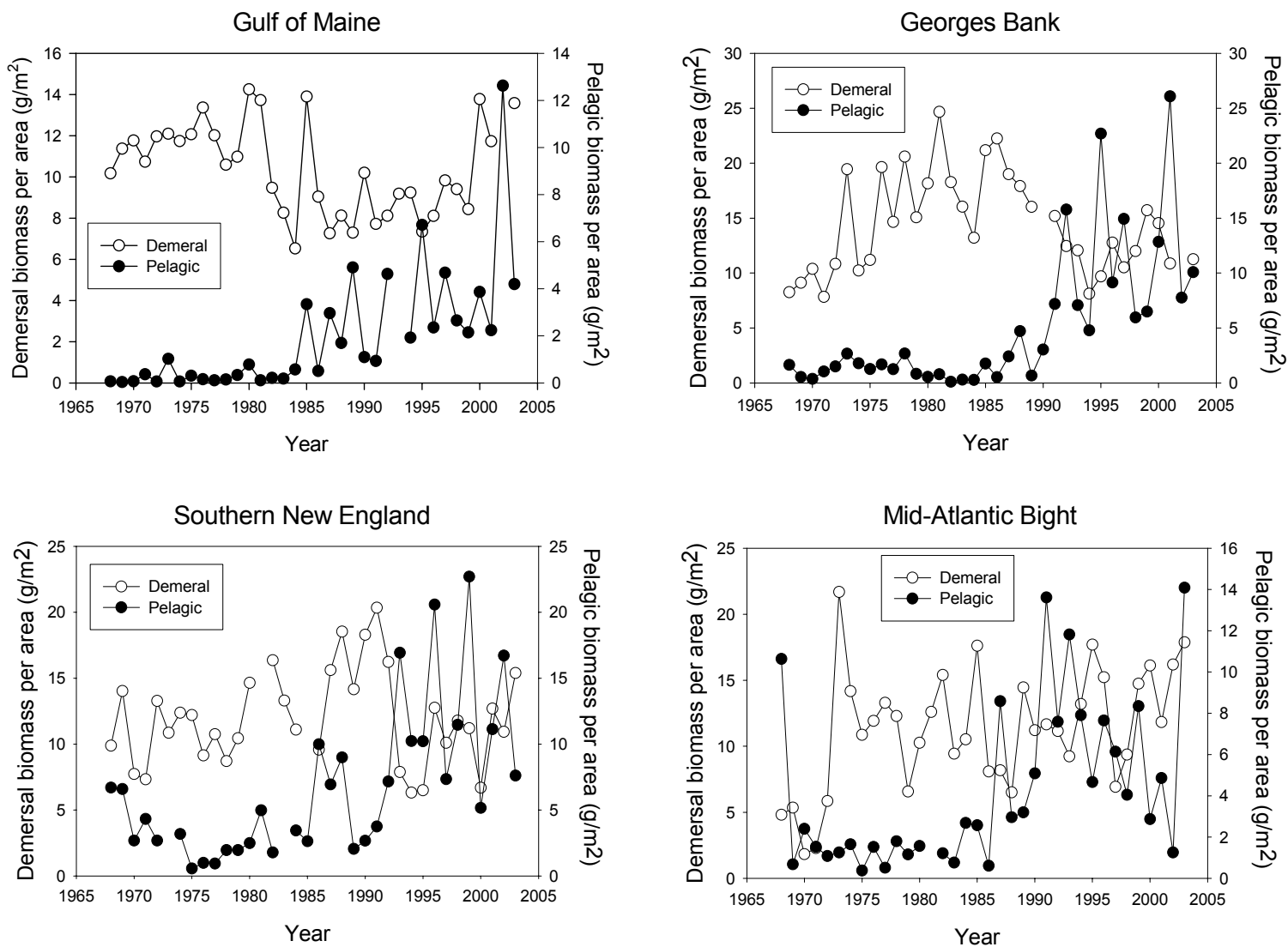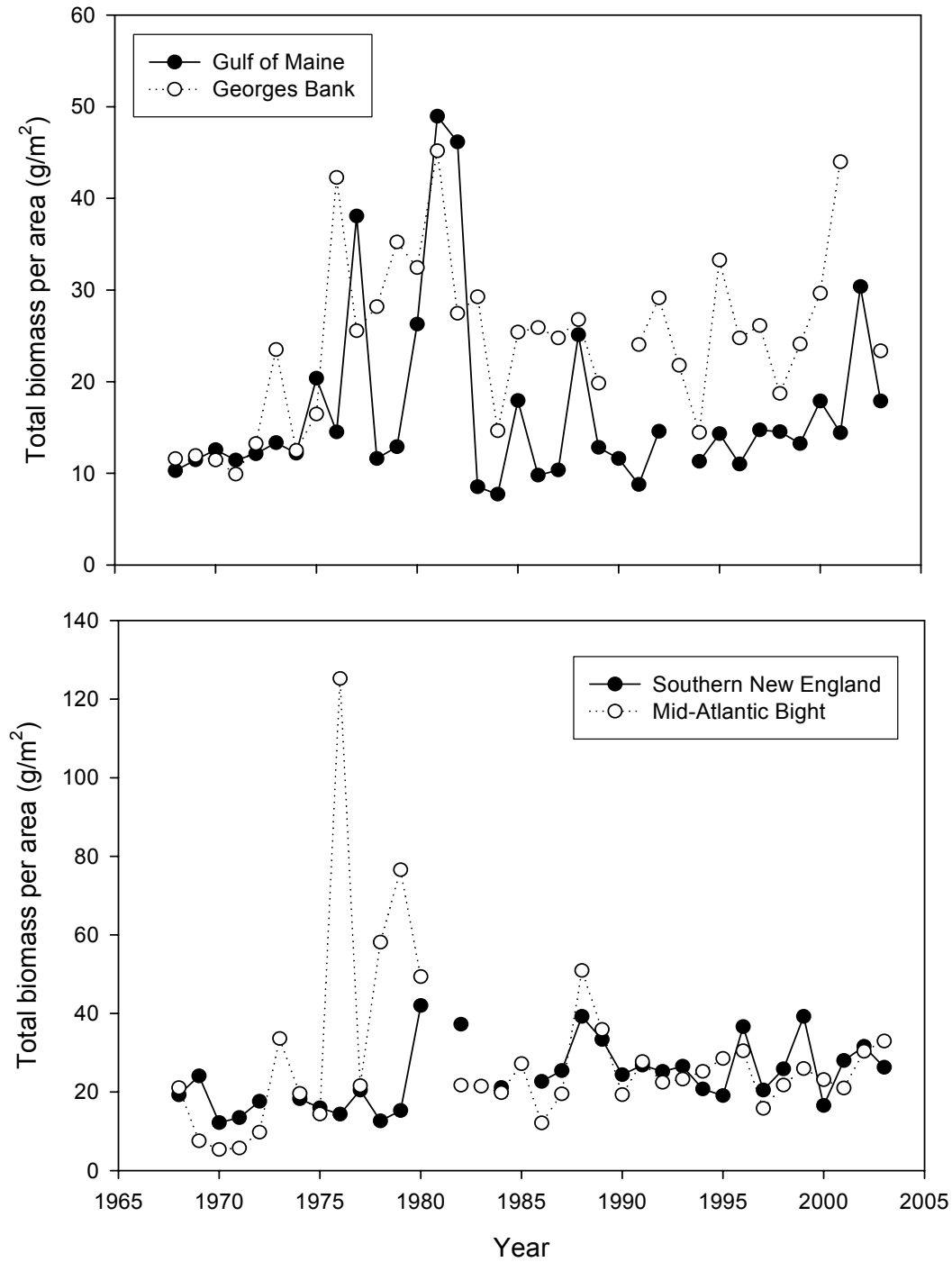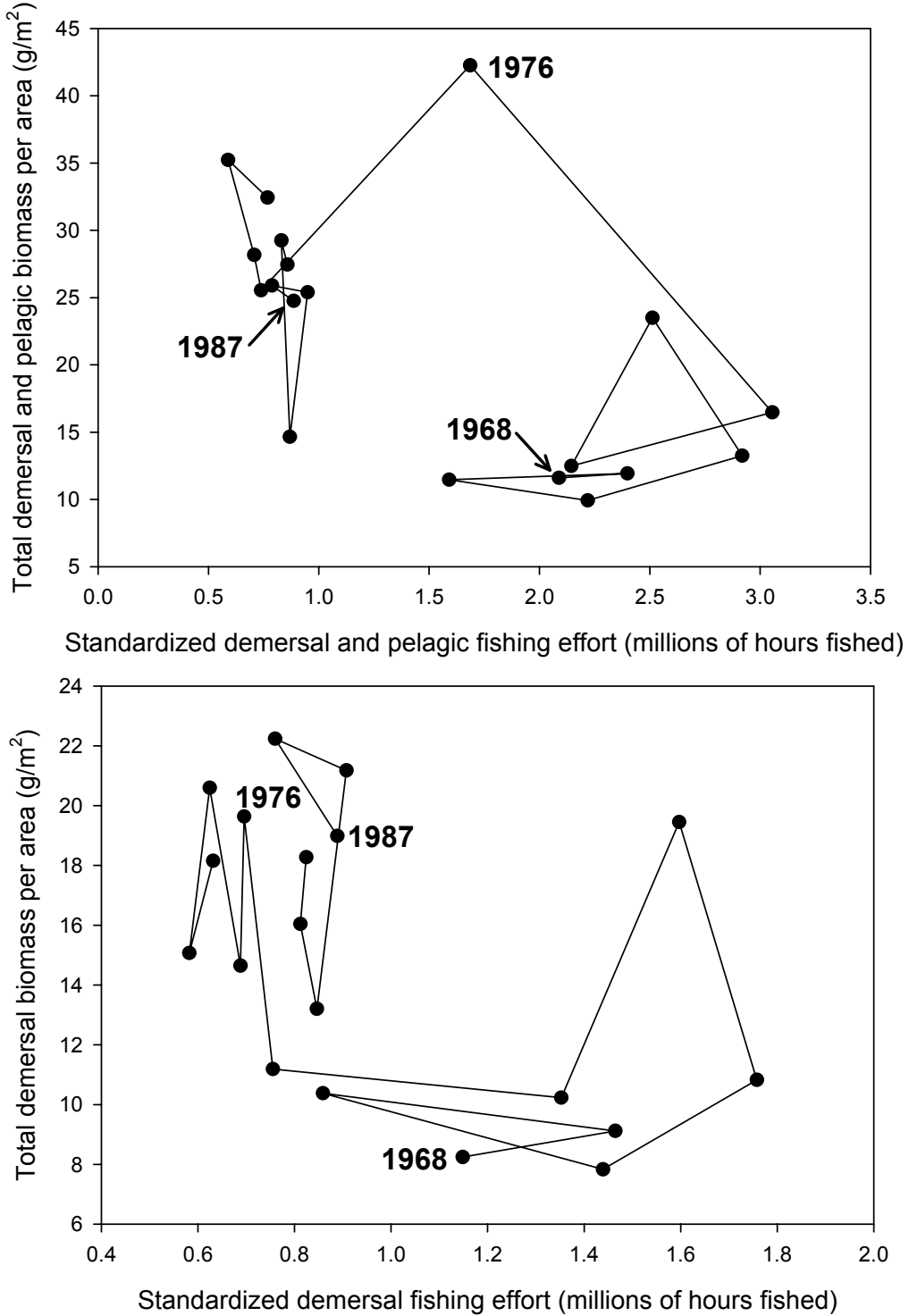
Figure 7. Trajectories of Georges Bank total and demersal biomass (g·m^{-2}) versus standardized total and demersal fishing effort estimates from Mayo et al. (1992) during 1968-1987 (no standardized effort estimates are available for 1981).

Appendix

Table A1. List of species in the demersal benthivore category.

Benthivores

Group	Species
Gadiformes	*Melanogrammus aeglefinus* *Urophycis chuss* *Urophycis regia* *Antimora rostrata* *Enchelyopus cimbrius* *Brosme brosme* *Gaidropsarus ensis* *Macrouridae* *Nezumia bairdi* *Macrourus berglax* *Coelorhynchus carminatus* *Otophidium omostigmum* *Ophidion marginatum* *Lepophidium profundorum* *Malacocephalus occidentalis* *Ophidion grayi* *Ophidion welshi*
Elasmobranchs	*Dasyatis centroura* *Etmopterus princeps* *Dasyatis say* *Myliobatis freminvillei* *Torpedo nobiliana* *Raja eglanteria* *Leucoraja garmani* *Malacoraja senta* *Dasyatis americana* *Rhinoptera bonasus*
Pleuronectiformes	*Poecilopsetta beani* *Hippoglossoides platessoides* *Paralichthys oblongus* *Limanda ferruginea* *Pseudopleuronectes americanus* *Glyptocephalus cynoglossus* *Scophthalmus aquosus* *Citharichthys arctifrons* *Monolene sessilicauda* *Etropus microstomus* *Trinectes maculatus*
Perciformes	*Macrorhamphosus scolopax* *Synagrops bellus* *Micropogonias undulatus* *Synagrops spinosus* *Orthopristis chrysoptera* *Stenotomus chrysops*

Perciformes continued	*Epigonus pandionis*
	Menticirrhus saxatilis
	Pogonias cromis
	Bairdiella chrysoura
	Leiostomus xanthurus
	Howella sherborni
	Lopholatilus chamaeleonticeps
	Tautogolabrus adspersus
	Tautoga onitis
	Astroscopus guttatus
	Lumpenus lumpretaeformis
	Lumpenus maculatus
	Ulvaria subbifurcata
	Mullus auratus
	Lycodes reticulatus
	Lycenchelys verrilli
	Cryptacanthodes maculatus
	Anarhichas lupus
	Macrozoarces americanus
	Nesiarchus nasutus
Scorpaeniformes	*Pontinus longispinis*
	Sebastes fasciatus
	Helicolenus dactylopterus
	Helicolenus maderensis
	Artediellus sp
	Cottidae
	Triglops murrayi
	Myoxocephalus scorpius
	Myoxocephalus octodecemspinosus
	Hemitripterus americanus
	Aspidophoroides monopterygius
	Myoxocephalus aenaeus
	Liparis inquilinus
	Eumicrotremus spinosus
	Prionotus carolinus
	Prionotus evolans
	Peristedion miniatum
	Triglidae
	Careproctus ranula
	Prionotus paralatus
Other Benthivores	*Myxine glutinosa*
	Antigonia capros
	Opsanus tau
	Dibranchus atlanticus
	Ogcocephalus corniger
	Chlorophthalmus sp
	Chlorophthalmus agassizi
	Gonostoma bathyphilum

	Gonostoma atlanticum
	Gonostoma elongatum
	Vinciguerria sp
	Polymetme thaeocoryla
	Chauliodus danae
	Parasudis truculenta
Other Benthivores	*Xenodermichthys copei*
continued	*Polymixia lowei*
	Polymixia nobilis
	Hoplostethus occidentalis
	Gephyroberyx darwini
	Saurida brasiliensis
	Bagre marinus
	Opsanus pardus
	Porichthys plectrodon

Table A2. List of species in the demersal piscivore category.

Piscivores

Group	Species
Gadiformes	*Merluccius albidus*
	Merluccius bilinearis
	Gadus morhua
	Pollachius virens
	Urophycis tenuis
	Urophycis chesteri
	Gadidae
	Merluccius sp
Elasmobranchs	*Carcharhinus obscurus*
	Centroscyllium fabricii
	Carcharhinus plumbeus
	Carcharias taurus
	Mustelus canis
	Scyliorhinus retifer
	Squalus acanthias
	Squatina dumeril
Other Piscivores	*Reinhardtius hippoglossoides*
	Hippoglossus hippoglossus
	Paralichthys dentatus
	Trichiurus lepturus
	Lophius americanus

Table A3. List of species in the demersal omnivore category.

Omnivores

Group	Species
Elasmosbranches	*Dipturus laevis* *Leucoraja ocellata* *Leucoraja erinacea* *Amblyraja radiata*
Other Omnivores	*Centropristis striata*

Table A4. List of species in the unclassifed southern demersal category.

Unclassified Demersal Species

Group	Species
Elasmobranchs	*Narcine brasiliensis* *Raja ackleyi* *Dipturus olseni* *Bathyraja spinicauda* *Raja texana* *Dasyatis sabina* *Dasyatis violacea* *Gymnura altavela* *Gymnura micrura* *Urolophus jamaicensis* *Myliobatis goodei* *Squalidae* *Etmopterus gracilispinis* *Etmopterus hillianus* *Centroscymnus coelolepis* *Breviraja plutonia* *Alopias vulpinus* *Alopias superciliosus* *Isurus paucus* *Carcharhinus isodon* *Carcharhinus altimus* *Carcharhinus longimanus* *Carcharhinus brevipinna* *Carcharhinus porosus* *Carcharhinus perezii* *Carcharhinus signatus* *Mustelus norrisi* *Triakis semifasciata* *Sphyrna media*
Gadiformes	*Laemonema barbatulum* *Ophidion beani* *Ophidion selenops*

Pleuronectiformes	*Ancylopsetta dilecta*
	Ancylopsetta quadrocellata
	Bothus lunatus
	Bothus ocellatus
	Chascanopsetta lugubris
	Citharichthys arenaceus
	Citharichthys cornutus
	Citharichthys macrops
	Citharichthys spilopterus
	Cyclopsetta fimbriata
	Engyophrys senta
	Etropus crossotus
	Etropus rimosus
	Gastropsetta frontalis
	Paralichthys albigutta
	Paralichthys lethostigma
	Paralichthys squamilentus
	Syacium gunteri
	Syacium micrurum
	Syacium papillosum
	Etropus sp
	Bothidae
	Paralichthys sp
	Citharichthys sp
	Bothus robinsi
	Citharichthys gymnorhinus
	Pleuronectidae
	Gymnachirus melas
	Symphurus civitatus
	Symphurus diomedianus
	Symphurus minor
	Symphurus marginatus
	Symphurus plagiusa
	Symphurus pusillus
	Symphurus urospilus
Perciformes	*Schultzea beta*
	Mycteroperca interstitialis
	Centropristis ocyurus
	Centropristis philadelphica
	Epinephelus inermis
	Diplectrum bivittatum
	Diplectrum formosum
	Epinephelus adscensionis
	Epinephelus drummondhayi
	Epinephelus flavolimbatus
	Epinephelus guttatus
	Epinephelus morio
	Epinephelus nigritus

Perciformes continued	*Epinephelus niveatus*
	Epinephelus striatus
	Hemanthias vivanus
	Mycteroperca bonaci
	Mycteroperca microlepis
	Mycteroperca phenax
	Mycteroperca venenosa
	Holanthias martinicensis
	Paranthias furcifer
	Hemanthias aureorubens
	Serraniculus pumilio
	Serranus annularis
	Serranus atrobranchus
	Serranus baldwini
	Serranus notospilus
	Serranus phoebe
	Serranus subligarius
	Serranidae
	Rypticus bistrispinus
	Priacanthus cruentatus
	Pristigenys alta
	Apogon maculatus
	Apogon pseudomaculatus
	Caulolatilus cyanops
	Lutjanus analis
	Lutjanus apodus
	Lutjanus buccanella
	Lutjanus campechanus
	Lutjanus griseus
	Lutjanus jocu
	Lutjanus synagris
	Lutjanus vivanus
	Ocyurus chrysurus
	Pristipomoides aquilonaris
	Rhomboplites aurorubens
	Lutjanidae
	Lobotes surinamensis
	Cookeolus japonicus
	Caulolatilus microps
	Caulolatilus chrysops
	Caulolatilus intermedius
	Malacanthus plumieri
	Epinephelus mystacinus
	Apogon aurolineatus
	Rypticus subbifrenatus
	Eucinostomus gula
	Gerreidae
	Archosargus probatocephalus

Perciformes continued	*Calamus bajonado*
	Calamus calamus
	Calamus leucosteus
	Calamus nodosus
	Calamus penna
	Calamus proridens
	Diplodus argenteus
	Diplodus holbrooki
	Lagodon rhomboides
	Pagrus sedecim
	Stenotomus caprinus
	Sparidae
	Cynoscion arenarius
	Cynoscion nebulosus
	Cynoscion nothus
	Equetus acuminatus
	Equetus lanceolatus
	Equetus punctatus
	Equetus umbrosus
	Larimus fasciatus
	Menticirrhus americanus
	Menticirrhus littoralis
	Sciaenops ocellatus
	Stellifer lanceolatus
	Sciaenidae
	Eucinostomus argenteus
	Pseudupeneus maculatus
	Upeneus parvus
	Kyphosus sectatrix
	Chaetodipterus faber
	Chaetodon aya
	Chaetodon capistratus
	Chaetodon ocellatus
	Chaetodon sedentarius
	Chaetodon striatus
	Holacanthus bermudensis
	Holacanthus ciliaris
	Holacanthus tricolor
	Pomacanthus arcuatus
	Abudefduf saxatilis
	Chromis enchrysurus
	Chromis insolata
	Pomacentrus leucostictus
	Bodianus pulchellus
	Clepticus parrae
	Decodon puellaris
	Halichoeres bathyphilus
	Halichoeres bivittatus

Perciformes continued	*Halichoeres caudalis*
	Halichoeres poeyi
	Halichoeres radiatus
	Hemipteronotus novacula
	Lachnolaimus maximus
	Labridae
	Chaetodontidae
	Chaetodon aculeatus
	Cryptotomus roseus
	Nicholsina usta
	Scarus coeruleus
	Sparisoma radians
	Scaridae
	Mugil liza
	Mugil gyrans
	Sphyraena barracuda
	Sphyraena borealis
	Sphyraena guachancho
	Opistognathus lonchurus
	Opistognathus maxillosus
	Bembrops gobioides
	Astroscopus y-graecum
	Xenocephalus egregius
	Kathetostoma albigutta
	Clinidae
	Parablennius marmoreus
	Chasmodes bosquianus
	Hypleurochilus geminatus
	Hypsoblennius hentz
	Hypsoblennius ionthas
	Blenniidae
	Ammodytes americanus
	Foetorepus agassizi
	Dormitator maculatus
	Bathygobius soporator
	Gobiosoma bosc
	Gobiidae
	Uranoscopidae
	Anisotremus virginicus
	Haemulon aurolineatum
	Haemulon carbonarium
	Haemulon plumieri
	Haemulidae
	Acanthurus bahianus
	Acanthurus chirurgus
	Acanthurus coeruleus
	Ariomma regulus
	Peprilus alepidotus

Perciformes continued	*Stromateidae*
	Trichiuridae
	Ruvettus pretiosus
	Lepidocybium flavobrunneum
	Pomacentrus variabilis
	Scombridae
	Gempylus serpens
	Cubiceps pauciradiatus
	Seriola fasciata
	Haemulon striatum
	Ariomma melanum
	Paralepidae
	Uraspis secunda
Scorpaeniformes	*Neomerinthe hemingwayi*
	Pontinus rathbuni
	Scorpaena agassizi
	Scorpaena brasiliensis
	Scorpaena calcarata
	Scorpaena dispar
	Scorpaena grandicornis
	Scorpaena plumieri
	Scorpaenidae
	Bellator brachychir
	Bellator egretta
	Bellator militaris
	Peristedion gracile
	Prionotus alatus
	Prionotus ophryas
	Prionotus roseus
	Prionotus longispinosus
	Prionotus rubio
	Prionotus scitulus
	Prionotus tribulus
	Myoxocephalus quadricornis
	Prionotus stearnsi
	Trachyscorpia cristulata
Tetradontiformes	*Balistidae*
	Parahollardia lineata
	Aluterus heudeloti
	Aluterus monoceros
	Aluterus schoepfi
	Aluterus scriptus
	Balistes vetula
	Canthidermis sufflamen
	Monacanthus ciliatus
	Lactophrys bicaudalis
	Lactophrys polygonia
	Lactophrys quadricornis

Tetradontiformes continued	Lactophrys trigonus
	Lactophrys triqueter
	Canthigaster rostrata
	Sphoeroides dorsalis
	Sphoeroides nephelus
	Sphoeroides spengleri
	Sphoeroides testudineus
	Chilomycterus antillarum
	Chilomycterus atinga
	Diodon holocanthus
	Diodon hystrix
	Tetraodontidae
	Sphoeroides pachygaster
Others	Xenolepidichthys dalgleishi
	Engraulidae
	Synodontidae
	Argentina striata
	Anchoa lyolepis
	Chaunax stigmaeus
	Gymnothorax saxicola
	Harengula jaguana
	Echiophis punctifer
	Gobiesox strumosus
	Ogcocephalus radiatus
	Gonostomatidae
	Anchoa cubana
	Anchoa nasuta
	Glossanodon pygmaeus
	Salmo salar
	Lophius gastrophysus
	Cyttopsis rosea
	Lophiiformes
	Gasterosteus wheatlandi
	Pungitius pungitius

Table A5. List of species in the pelagics category.

Pelagics

Group	Species
Commercial Finfish	Clupea harengus
	Scomber scombrus
	Peprilus triacanthus
Squid	Cephalopoda
	Illex illecebrosus
	Loligo pealeii
Anadromous	Alosa pseudoharengus
	Alosa aestivalis

Anadromous continued	*Alosa sapidissima* *Alosa mediocris*
Meso-Pelagics	*Myctophidae* *Maurolicus sp*
Unclassified Pelagics	*Etrumeus teres* *Brevoortia tyrannus* *Osmerus mordax* *Argentina silus* *Menidia menidia* *Ammodytes dubius* *Anchoa mitchilli* *Anchoa hepsetus* *Ablennes hians* *Scomber japonicus* *Selene setapinnis* *Scomberesox saurus* *Decapterus macarellus* *Selar crumenophthalmus* *Decapterus punctatus* *Trachurus lathami* *Ariomma bondi* *Opisthonema oglinum* *Sardinella aurita* *Hemiramphus brasiliensis* *Mugil cephalus* *Mugil curema*