14. Demersals (benthivores, omnivores, piscivores) and Medium Pelagics

Jon K.T. Brodziak, Christopher M. Legault, and Laurel A. Col (nodes #22-24, 21)

Background

Three groups of demersal species were formed based on feeding preferences described in Collette and Klein-MacPhee (2002). These are: benthivores, piscivores, and omnivores (includes 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 (Table 14.1). The demersal piscivore group included species that feed primarily on fishes. This group included gadiformes, elasmobranchs, and other piscivores (Table 14.2). The unclassified demersals was a large group composed of either omnivorous species that fed opportunistically on both benthos and fish (Table 14.3), or unclassified southern demersal species whose food habits were not reported in Collette and Klein-MacPhee (2002; Table 14.4).

Data Sources

Annual research survey data were collected from 1968-2003 to estimate demersal and pelagic biomasses using a stratified random sampling design (Azarovitz 1981).

Quantitative Approach for Biomass Estimates

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):

(EQ. 14.1) $$B = \frac{I}{Q}$$

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 Equation 14.1. 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 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 | Q)≡L(D | Q).

(EQ. 14.2) $$p(Q \mid D) = p(Q)p(D \mid Q)$$

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

(EQ. 14.3) $$p(Q|D) = \frac{p(Q,D)}{p(D)} = \frac{p(Q)p(D|Q)}{p(D)}$$

where the integrated likelihood p(D) was the constant

(EQ. 14.4) $$p(D) = \int p(Q)p(D|Q)dQ$$

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

(EQ. 14.5) $$p(Q|D) \propto p(Q)p(D|Q)$$

Markov Chain Monte Carlo (MCMC) simulation (Gilks *et al.* 1996) was applied to numerically generate posterior samples from Equation. 14.5. 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 Equation 14.3. 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 for inference (50,000 from each chain). 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

(EQ. 14.6) $$E\left[B_j \mid D\right] \approx \frac{1}{N}\sum_{T=1}^{N} B_j\left(Q^T\right)$$

Informative Priors

Prior information on NEFSC research survey catchabilities was 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 demersal species groups was assumed to be a gamma distribution with shape (r) and scale (μ) parameters.

(EQ. 14.7) $$p\left(Q|r,\mu\right) \sim Gamma\left(r,\mu\right) = \mu^r Q^{r-1}\frac{e^{-\mu Q}}{\Gamma(r)} \quad for\, Q > 0$$

This choice provided a flexible positive distribution with mean equal to E[Q] = r/μ 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 the "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%.

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 14.2). 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 calculation factor. There were a total of 12 catchability observations derived from assessment data (Table 14.2). 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 (e.g., American plaice, *Hippoglossoides platessoides*), but not for 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.

Likelihood of Catchability Observations

The likelihood of a single catchability observation was a gamma distribution (Equation 14.3) with shape and scale parameters set by the informative priors. Seven demersal subgroups did not have any catchability observations (Table 14.2). 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 14.2). 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

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

(EQ. 14.8)

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})

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

(EQ. 14.9)

We removed outliers based on the biomass production anomalies. For demersal species groups, an observed value was an outlier if $B^{ANOM} > 3$. 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 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 biomass differed among regions. Last, the average total production of demersal biomass was computed for each region to determine differences in total biomass production among regions.

Example Results

Average biomass production

Total demersal biomass production differed among regions (Figure 14.1). 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 (Figure 14.1). 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 (Figure 14.1). 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%).

Production/Growth/Reproduction

Production for demersals and medium pelagics was estimated using age-based data for a small number of assessed stocks to confirm literature values for the P:B ratio (Cohen *et al.* 1982; Sissenwine 1987; Savenkoff *et al.* 2004). Two approaches were used to estimate the P:B ratios from virtual population analysis results: age-based growth and a production model. The age-based growth approach computed the change in weight at age for each cohort in a given year and multiplied these values by the average biomass for that age. Summing these values produced an estimate of production which was then divided by the beginning of the year biomass to generate an estimate of the P:B ratio. The production model approach calculated production as the total catch plus the change in biomass each year and then divided that by the biomass to produce a P:B ratio. Results for Georges Bank cod, haddock and yellowtail flounder ranged from 0.34 to 0.48 for the age-based growth approach and ranged from 0.35 to 0.59 for the production model approach. These results agreed in general with the literature values for demersals and medium pelagics. The selected values for the P:B ratio varied by group: demersal benthivores and omnivores had a ratio of 0.45 while demersal piscivores and medium pelagics had a ratio of 0.55.

Consumption

Consumption was estimated using the methods described in Section 22: Consumption and Diet Composition Matrix, based on NEFSC research survey observations. Resulting C:B ratios for the Gulf of Maine ecoregion were on the order of 0.6 to 3.0.

References

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

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

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

Brown, JH; Gillooly, JF; Allen, AP; West, GB. 2004. Towards a metabolic theory of ecology. *Ecol.* 85(7):1771-1789.

Choi, JS; Frank, KT; Leggett, WC; Drinkwater, K. 2004. Transition to an alternate state in a continental shelf ecosystem. *Can. J. Fish. Aqua. Sci*. 61:505-510.

Clark, SH; Brown, BE. 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.

Cohen, EB; Grosslein, MD; Sissenwine, MP; Steimle, F; Wright, WR. 1982. Energy budget of Georges Bank. Canadian Special Publication of Fisheries and Aquatic Sciences. Workshop on Multispecies Approaches to Fisheries Management Advice, St. John's, Newfoundland.

Collette, BB; Klein-MacPhee, G, eds. 2002. *Bigelow and Schroeder's Fishes of the Gulf of Maine, 3rd Ed.* Washington, D.C.: Smithsonian Institution Press; 748 p.

Edwards, RL. 1968. Fishery resources of the North Atlantic area. *In:* Gilbert, DW, ed. *The future of the fishing industry of the United States*. Univ. of Washington Publications in Fisheries. 4:52-60.

Fogarty, MJ; Cohen, EB; Michaels, WL; Morse, WW. 1991. Predation and the regulation of sand lance populations: an exploratory analysis. *ICES Mar. Sci. Symp*. 193:120-124.

Fogarty, MJ; Murawski, SA. 1998. Large-scale disturbance and the structure of marine ecosystems: fishery impacts on Georges Bank. *Ecol*. Appl. 8(1) Suppl. S6-S22 p.

Gilks, WR; Richardson, S; Spiegelhalter, DG, eds. 1996. *Markov chain monte carlo in practice*. London, UK: Chapman and Hall; 486 p.

Harley, SJ; Myers, R; Barrowman, N; Bowenand, K; Admiro, R. 2001. Estimation of research trawl survey catchability for biomass reconstruction of the eastern Scotian Shelf. *Can. Sci. Advis. Sec. Res. Doc*. 2001/084; 54 p.

Hatfield, EMC; Hanlon, RT; Forsythe, JW; Grist, EPM. 2001. Laboratory testing of a growth hypothesis for juvenile squid *Loligo pealeii* (Cephalopoda: Loliginidae). *Can. J. Fish. Aquat. 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; p. 571-588.

Link, JS; Garrison, LP. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. *Fish. Res*. 55:71-86.

Mayo, RK; Fogarty, MJ; Serchuk, FM. 1992. Aggregate fish biomass and yield on Georges Bank, 1960-87. *J. Northw. Atl. Fish. Sci*. 14:59-78.

Mountain, DG; Holzwarth, TJ. 1989. Surface and bottom temperature distribution for the northeast continental shelf. *NOAA Technical Memorandum*. NMFS-F/NEC-73; 32 p. Available from NEFSC Library, 166 Water St., Woods Hole, MA 02543.

Mountain, DG; Taylor, MH; Bascuñán, C. 2004. Revised Procedures for Calculating Regional Average Water Properties for Northeast Fisheries Science Center Cruises. Woods Hole, MA. *Northeast Fish. Sci. Cent. Ref. Doc*. 04-08; 62 p.

Murawski, SA; Brown, R; Lai, H-L; Rago, PJ; 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 p. 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). Woods Hole, MA. *Northeast Fish. Sci. Cent. Ref. Doc*. 00-03; 37 p.

NEFSC. 2002. Assessment of 20 northeast groundfish stocks through 2001. A report of the Groundfish Assessment Review Meeting. Woods Hole, MA. *Northeast Fish. Sci. Cent. Ref. Doc.* 02-16; 478 p.

NEFSC. 2003. 37th Northeast Regional Stock Assessment Workshop (37th SAW) Stock Assessment Review Committee (SARC) Consensus Summary of Assessments. Woods Hole, MA. *Northeast Fish. Sci. Cent. Ref. Doc.* 03-16; 603 p.

NEFSC. 2004. Atlantic Butterfish. 38th Northeast Regional Stock Assessment Workshop (38th SAW). Woods Hole, MA. *Northeast Fish. Sci. Cent. Ref. Doc.* 04-03; 72 p.

O'Reilly, J; Evans-Zetlin, C; Busch, D. 1987. Primary production. *In:* Backus, R; Price, R; Bourne, D, eds. *Georges Bank.* Cambridge, MA: MIT Press; p. 220-233.

Overholtz, WJ; Friedland, KD. 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, WJ; Jacobson, LD; Melvin, GD; Cieri, M; Power, M; Libby, D; Clark, K. 2004. Stock assessment of the Gulf of Maine-Georges Bank Atlantic herring complex, 2003. Woods Hole, MA. *Northeast Fish. Sci. Cent. Ref. Doc.* 04-06; 290 p.

Savenkoff, C; Castonguay, M; Despatie, S-P; Chabot, D; Hammill, MO. 2004. Inverse modelling of trophic flows through an entire ecosystem: the northern Gulf of St. Lawrence in the mid-1980s. *Can. J. Fish. Aquat. Sci*. 61: 2194–2214.

Sissenwine, MP. 1987. Fish and squid production. *In:* Backus, R; Price, R; Bourne, D, eds. *Georges Bank.* Cambridge, MA: MIT Press; p. 347-350.

Spiegelhalter, D; Thomas, A; Best, N; 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. Wood Hole, MA. *Fish. Sci. Cent. Ref. Doc.* 03-09. 190 p.

Wigley, S; Brodziak, JKT; Col, L. 2003. Assessment of the Gulf of Maine and Georges Bank witch flounder stock for 2003. Wood Hole, MA. *Fish. Sci. Cent. Ref. Doc.* 03-14; 194 p.

Table 14.1. List of species in the demersal benthivore category.

Demersal Benthivores				
Gadiformes	Elasmobranchs	Perciformes	Scorpaeniformes	Others
Melanogrammus aeglefinus	*Dasyatis centroura*	*Macrorhamphosus scolopax*	*Pontinus longispinis*	*Myxine glutinosa*
Urophycis chuss	*Etmopterus princeps*	*Synagrops bellus*	*Sebastes fasciatus*	*Antigonia capros*
Urophycis regia	*Dasyatis say*	*Micropogonias undulatus*	*Helicolenus dactylopterus*	*Opsanus tau*
Antimora rostrata	*Myliobatis freminvillei*	*Synagrops spinosus*	*Helicolenus maderensis*	*Dibranchus atlanticus*
Enchelyopus cimbrius	*Torpedo nobiliana*	*Orthopristis chrysoptera*	*Artediellus sp.*	*Ogcocephalus corniger*
Brosme brosme	*Raja eglanteria*	*Stenotomus chrysops*	*Cottidae*	*Chlorophthalmus sp*
Gaidropsarus ensis	*Leucoraja garmani*	*Epigonus pandionis*	*Triglops murrayi*	*Chlorophthalmus agassizi*
Macrouridae	*Malacoraja senta*	*Menticirrhus saxatilis*	*Myoxocephalus scorpius*	*Gonostoma bathyphilum*
Nezumia bairdi	*Dasyatis americana*	*Pogonias cromis*	*Myoxocephalus octodecemspinosus*	*Gonostoma atlanticum*
Macrourus berglax	*Rhinoptera bonasus*	*Bairdiella chrysoura*	*Hemitripterus americanus*	*Gonostoma elongatum*
Coelorhynchus carminatus		*Leiostomus xanthurus*	*Aspidophoroides monopterygius*	*Vinciguerria sp*
Otophidium omostigmum		*Howella sherborni*	*Myoxocephalus aenaeus*	*Polymetme thaeocoryla*
Ophidion marginatum	Pleuronectiformes	*Lopholatilus chamaeleonticeps*	*Liparis inquilinus*	*Chauliodus danae*
Lepophidium profundorum	*Poecilopsetta beani*	*Tautogolabrus adspersus*	*Eumicrotremus spinosus*	*Parasudis truculenta*
Malacocephalus occidentalis	*Hippoglossoides platessoides*	*Tautoga onitis*	*Prionotus carolinus*	*Xenodermichthys copei*
Ophidion grayi	*Paralichthys oblongus*	*Astroscopus guttatus*	*Prionotus evolans*	*Polymixia lowei*
Ophidion welshi	*Limanda ferruginea*	*Lumpenus lumpretaeformis*	*Peristedion miniatum*	*Polymixia nobilis*
	Pseudopleuronectes americanus	*Lumpenus maculatus*	*Triglidae*	*Hoplostethus occidentalis*
	Glyptocephalus cynoglossus	*Ulvaria subbifurcata*	*Careproctus ranula*	*Gephyroberyx darwini*
	Scophthalmus aquosus	*Mullus auratus*	*Prionotus paralatus*	*Saurida brasiliensis*
	Citharichthys arctifrons	*Lycodes reticulatus*		*Bagre marinus*
	Monolene sessilicauda	*Lycenchelys verrilli*		*Opsanus pardus*
	Etropus microstomus	*Cryptacanthodes maculatus*		*Porichthys plectrodon*
	Trinectes maculatus	*Anarhichas lupus*		
		Macrozoarces americanus		
		Nesiarchus nasutus		

Table 14.2. List of species in the demersal piscivore category.

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

Table 14.3. List of species in the demersal omnivore category.

Demersal Omnivores	
Elasmobranchs	Others
Dipturus laevis	*Centropristis striata*
Leucoraja ocellata	
Leucoraja erinacea	
Amblyraja radiata	

Table 14.4. List of species in the unclassified southern demersal category.

Unclassified Southern Demersal Species			
Perciformes	Perciformes (Cont.)	Perciformes (Cont.)	Tetradontiformes
Schultzea beta	*Epinephelus mystacinus*	*Halichoeres caudalis*	*Balistidae*
Mycteroperca interstitialis	*Apogon aurolineatus*	*Halichoeres poeyi*	*Parahollardia lineata*
Centropristis ocyurus	*Rypticus subbifrenatus*	*Halichoeres radiatus*	*Aluterus heudeloti*
Centropristis philadelphica	*Eucinostomus gula*	*Hemipteronotus novacula*	*Aluterus monoceros*
Epinephelus inermis	*Gerreidae*	*Lachnolaimus maximus*	*Aluterus schoepfi*
Diplectrum bivittatum	*Archosargus probatocephalus*	*Labridae*	*Aluterus scriptus*
Diplectrum formosum	*Perciformes*	*Chaetodontidae*	*Balistes vetula*
Epinephelus adscensionis	*Calamus bajonado*	*Chaetodon aculeatus*	*Canthidermis sufflamen*
Epinephelus drummondhayi	*Calamus calamus*	*Cryptotomus roseus*	*Monacanthus ciliatus*
Epinephelus flavolimbatus	*Calamus leucosteus*	*Nicholsina usta*	*Lactophrys bicaudalis*
Epinephelus guttatus	*Calamus nodosus*	*Scarus coeruleus*	*Lactophrys polygonia*
Epinephelus morio	*Calamus penna*	*Sparisoma radians*	*Lactophrys quadricornis*
Epinephelus nigritus	*Calamus proridens*	*Scaridae*	*Lactophrys trigonus*
Epinephelus niveatus	*Diplodus argenteus*	*Mugil liza*	*Lactophrys triqueter*
Epinephelus striatus	*Diplodus holbrooki*	*Mugil gyrans*	*Canthigaster rostrata*
Hemanthias vivanus	*Lagodon rhomboides*	*Sphyraena barracuda*	*Sphoeroides dorsalis*
Mycteroperca bonaci	*Pagrus sedecim*	*Sphyraena borealis*	*Sphoeroides nephelus*
Mycteroperca microlepis	*Stenotomus caprinus*	*Sphyraena guachancho*	*Sphoeroides spengleri*
Mycteroperca phenax	*Sparidae*	*Opistognathus lonchurus*	*Sphoeroides testudineus*
Mycteroperca venenosa	*Cynoscion arenarius*	*Opistognathus maxillosus*	*Chilomycterus antillarum*
Holanthias martinicensis	*Cynoscion nebulosus*	*Bembrops gobioides*	*Chilomycterus atinga*
Paranthias furcifer	*Cynoscion nothus*	*Astroscopus y-graecum*	*Diodon holocanthus*
Hemanthias aureorubens	*Equetus acuminatus*	*Xenocephalus egregius*	*Diodon hystrix*
Serraniculus pumilio	*Equetus lanceolatus*	*Kathetostoma albigutta*	*Tetraodontidae*
Serranus annularis	*Equetus punctatus*	*Clinidae*	*Sphoeroides pachygaster*
Serranus atrobranchus	*Equetus umbrosus*	*Hypsoblennius ionthas*	
Serranus baldwini	*Larimus fasciatus*	*Blenniidae*	
Serranus notospilus	*Menticirrhus americanus*	*Ammodytes americanus*	
Serranus phoebe	*Menticirrhus littoralis*	*Foetorepus agassizi*	
Serranus subligarius	*Sciaenops ocellatus*	*Dormitator maculatus*	
Serranidae	*Stellifer lanceolatus*	*Bathygobius soporator*	
Rypticus bistrispinus	*Sciaenidae*	*Gobiosoma bosc*	
Priacanthus cruentatus	*Eucinostomus argenteus*	*Gobiidae*	
Pristigenys alta	*Pseudupeneus maculatus*	*Uranoscopidae*	
Apogon maculatus	*Upeneus parvus*	*Anisotremus virginicus*	
Apogon pseudomaculatus	*Kyphosus sectatrix*	*Haemulon aurolineatum*	
Caulolatilus cyanops	*Chaetodipterus faber*	*Haemulon carbonarium*	
Lutjanus analis	*Chaetodon aya*	*Haemulon plumieri*	
Lutjanus apodus	*Chaetodon capistratus*	*Haemulidae*	
Lutjanus buccanella	*Chaetodon ocellatus*	*Acanthurus bahianus*	
Lutjanus campechanus	*Chaetodon sedentarius*	*Acanthurus chirurgus*	
Lutjanus griseus	*Chaetodon striatus*	*Acanthurus coeruleus*	
Lutjanus jocu	*Holacanthus bermudensis*	*Ariomma regulus*	
Lutjanus synagris	*Holacanthus ciliaris*	*Peprilus alepidotus*	
Lutjanus vivanus	*Holacanthus tricolor*	*Stromateidae*	
Ocyurus chrysurus	*Pomacanthus arcuatus*	*Trichiuridae*	
Pristipomoides aquilonaris	*Abudefduf saxatilis*	*Ruvettus pretiosus*	
Rhomboplites aurorubens	*Chromis enchrysurus*	*Lepidocybium flavobrunneum*	
Lutjanidae	*Chromis insolata*	*Pomacentrus variabilis*	
Lobotes surinamensis	*Pomacentrus leucostictus*	*Scombridae*	
Cookeolus japonicus	*Bodianus pulchellus*	*Gempylus serpens*	
Caulolatilus microps	*Clepticus parrae*	*Cubiceps pauciradiatus*	
Caulolatilus chrysops	*Decodon puellaris*	*Seriola fasciata*	
Caulolatilus intermedius	*Halichoeres bathyphilus*	*Haemulon striatum*	
Malacanthus plumieri	*Halichoeres bivittatus*	*Ariomma melanum*	
		Paralepidae	
		Uraspis secunda	
		Parablennius marmoreus	
		Chasmodes bosquianus	
		Hypleurochilus geminatus	
		Hypsoblennius hentz	

Table 14.4, continued.

Pleuronectiformes	Elasmobranchs	Scorpaeniformes	Gadiformes
Ancylopsetta dilecta	*Narcine brasiliensis*	*Neomerinthe hemingwayi*	*Laemonema barbatulum*
Ancylopsetta quadrocellata	*Raja ackleyi*	*Pontinus rathbuni*	*Ophidion beani*
Bothus lunatus	*Dipturus olseni*	*Scorpaena agassizi*	*Ophidion selenops*
Bothus ocellatus	*Bathyraja spinicauda*	*Scorpaena brasiliensis*	
Chascanopsetta lugubris	*Raja texana*	*Scorpaena calcarata*	
Citharichthys arenaceus	*Dasyatis sabina*	*Scorpaena dispar*	**Others**
Citharichthys cornutus	*Dasyatis violacea*	*Scorpaena grandicornis*	
Citharichthys macrops	*Gymnura altavela*	*Scorpaena plumieri*	*Xenolepidichthys dalgleishi*
Citharichthys spilopterus	*Gymnura micrura*	*Scorpaenidae*	*Engraulidae*
Cyclopsetta fimbriata	*Urolophus jamaicensis*	*Bellator brachychir*	*Synodontidae*
Engyophrys senta	*Myliobatis goodei*	*Bellator egretta*	*Argentina striata*
Etropus crossotus	*Squalidae*	*Bellator militaris*	*Anchoa lyolepis*
Etropus rimosus	*Etmopterus gracilispinis*	*Peristedion gracile*	*Chaunax stigmaeus*
Gastropsetta frontalis	*Etmopterus hillianus*	*Prionotus alatus*	*Gymnothorax saxicola*
Paralichthys albigutta	*Centroscymnus coelolepis*	*Prionotus ophryas*	*Harengula jaguana*
Paralichthys lethostigma	*Breviraja plutonia*	*Prionotus roseus*	*Echiophis punctifer*
Paralichthys squamilentus	*Alopias vulpinus*	*Prionotus longispinosus*	*Gobiesox strumosus*
Syacium gunteri	*Alopias superciliosus*	*Prionotus rubio*	*Ogcocephalus radiatus*
Syacium micrurum	*Isurus paucus*	*Prionotus scitulus*	
Syacium papillosum	*Carcharhinus isodon*	*Prionotus tribulus*	
Etropus sp	*Carcharhinus altimus*	*Myoxocephalus quadricornis*	
Bothidae	*Carcharhinus longimanus*	*Prionotus stearnsi*	
Paralichthys sp.	*Carcharhinus brevipinna*	*Trachyscorpia cristulata*	
Citharichthys sp.	*Carcharhinus porosus*		
Bothus robinsi	*Carcharhinus perezii*		
Pleuronectiformes	*Carcharhinus signatus*		
Citharichthys gymnorhinus	*Mustelus norrisi*		
Pleuronectidae	*Triakis semifasciata*		
Gymnachirus melas	*Sphyrna media*		
Symphurus civitatus			
Symphurus diomedianus			
Symphurus minor			
Symphurus marginatus			
Symphurus plagiusa			
Symphurus pusillus			
Symphurus urospilus			

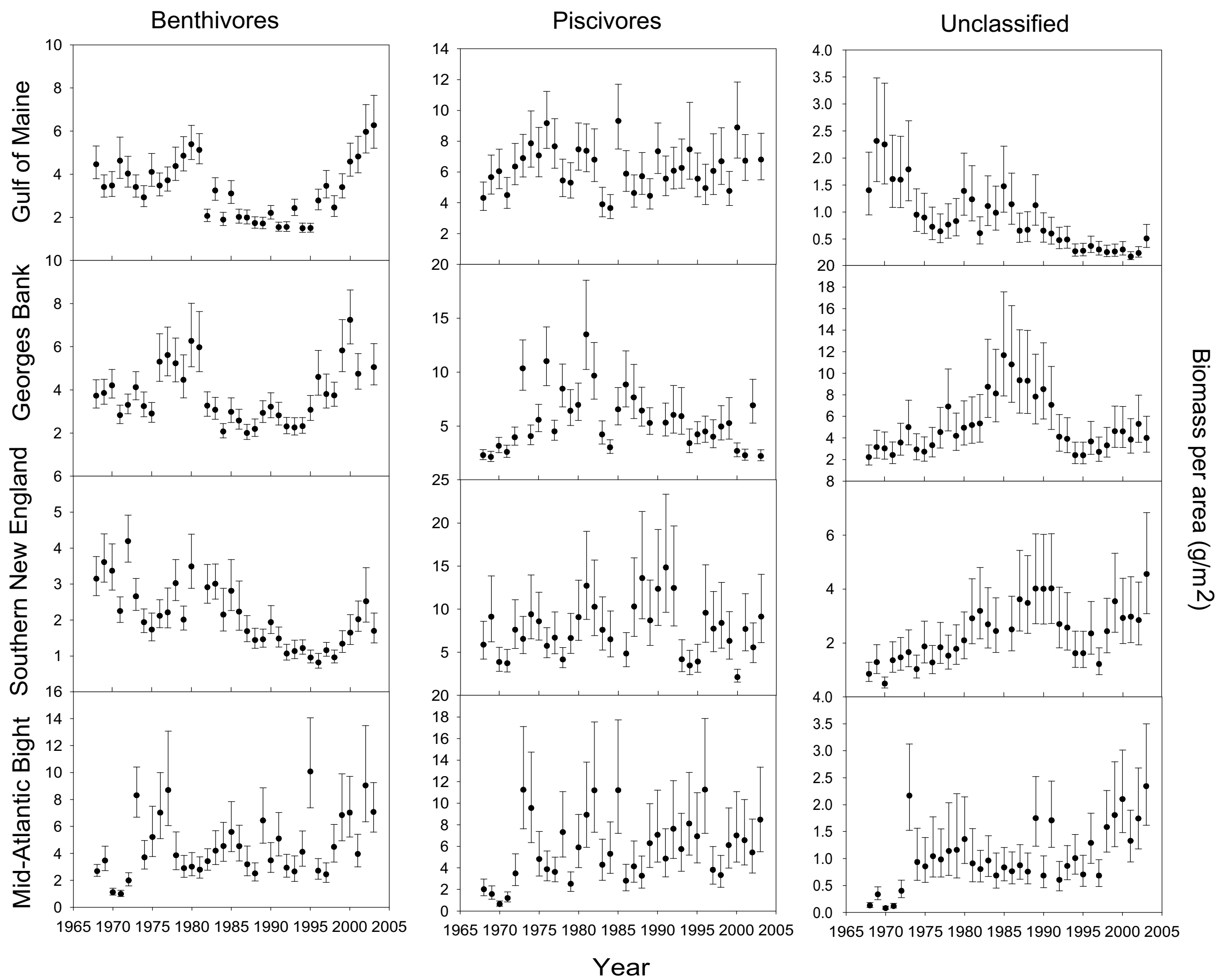

Figure 14.1. Time series of annual demersal biomass production (g m^{-2}) by benthivores, piscivores, and unclassified species in four regions of the Northeast United States Continental Shelf Ecosystem (Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight) during 1968-2003.