Transactions of the American Fisheries Society 120:459–473, 1991

Empirical Model of the Trophic Basis for Fishery Yield in Coastal Waters of the Eastern USA

D. S. PETERS[1] AND W. E. SCHAAF

National Marine Fisheries Service, Southeast Fisheries Center
Beaufort Laboratory, Beaufort, North Carolina 28516, USA

Abstract.—A synthesis of information describing the trophic basis for production of marine fishery yield along the east coast of the USA from New York through Georgia is presented. It includes a documentation of the species composition and magnitude of fishery harvest, a delineation of the major food chains, and an estimate of the flow rates of organic matter through populations of yield species. In order to place the information on fishery food webs in appropriate context, we related it to primary production within the system and trophic structure of other systems that have been described. We conclude that (1) algal production is inadequate to support the existing system, and vascular plant production is required; (2) detritus, a frequent dietary constituent, retains at least 42% of the organic material from which it was derived, when it is ingested; (3) the system efficiently converts available organic matter to harvested species through direct paths; and (4) evaluations of fish production in this system may be advanced most rapidly by research on detritus production and use, species composition and diets of forage fish, and mortality rates of both forage fish and prerecruits of yield species.

Our purpose is to summarize the role of exploited species in the flow of energy and material through the food web of a large coastal ecosystem. The methods represent a synthesis of available ecological and fishery data, with emphasis on the latter. We present a model that quantifies the relationship between primary production and fishery yield (both finfish and shellfish) for a large portion of the U.S. east coast, a system that includes tidal marshes, estuaries, and coastal waters in an 8-km-wide band from New York through Georgia. The model elucidates the flow of material through the food web supporting the fishery, demonstrates the energetic constraints on production of harvested species, and identifies critical areas of research needed to more fully understand the relationship. We have not attempted to model detailed ecological processes or to achieve mass balance at each trophic step. Rather, we have taken a broad view of the entire production system, and our approach is empirical (Rigler 1982). We describe, in a general way, the structural characteristics of a fishery-sustaining ecosystem without attempting to describe the detailed interactions that may operate among the components of the system. This contribution represents the first step of Kerr's (1982) external analysis. Although we have not reached the predictive stage concerning many emergent properties of the system, such as total fishery yield, the analysis does provide insight into the operation of the system.

Our model development has been "top down": we started with fishery yield, which is known with fair accuracy, and worked backward to determine the production required at each step of the trophic sequence leading to the observed yield. We computed the food requirements for each trophic step without attempting to balance material or energy flows at each transfer. Emphasis was on empirical observation, not on ecological or physiological theory. Data on primary production allowed us to evaluate information about food chains that support fisheries and set limits on the magnitude of undescribed trophic flows within the system. We paid particular attention to selecting appropriate boundaries of the system but could not avoid some arbitrary delineations.

From this simple approach, several fundamental conclusions emerge regarding the structure and function of this fishery system. The total yield is high compared with published estimates from other large systems. High yield can be explained by high primary production and short, efficient food chains leading to the harvested species. We used available dietary information conservatively to describe the food chains, and probably underestimated the cost of fish production, cost being the amount of primary production required to produce the fish. Nevertheless, the yield evidently requires a substantial fraction of primary production. Much of the primary production is by vas-

[1] Order of authorship determined by the flip of a coin.

TABLE 1.—The harvested species and the sources of size-specific dietary information that document trophic relationships in the model of production of fishery species in coastal waters of the eastern USA; NA means not available.

Common name	Scientific name	Dietary studies	Size (mm)
		Finfish	
Atlantic croaker	*Micropogonias undulatus*	Darnell (1958)	50–150
		Hansen (1969)	<76–173
		Schwartz et al. (1980)	40–150
Atlantic mackerel	*Scomber scombrus*	Edwards and Bowman (1979)	NA
		Mid-Atlantic Fishery Management Council (1978)	NA
Atlantic menhaden	*Brevoortia tyrannus*	Lewis and Peters (1984)	50–150
		Mulkana (1966)	<80
		Darnell (1964)	NA
		June and Carlson (1971)	28–94
		Jeffries (1975)	40–60
Black drum	*Pogonias cromis*	Darnell (1958)	116–218
Bluefish	*Pomatomus saltatrix*	Lassiter (1962)	<200–900
		Grant (1962)	50–200
King mackerel	*Scomberomorus cavalla*	Naughton and Saloman (1981)	300–1,600
		Saloman and Naughton (1983)	100–300
Northern puffer	*Sphoeroides maculatus*	Linton (1905)	NA
		Shipp and Yerger (1969)	NA
Red drum	*Sciaenops ocellatus*	Darnell (1958)	184–625
		Boothby and Avault (1971)	250–932
		Bass and Avault (1975)	50–190
Spanish mackerel	*Scomberomorus maculatus*	Naughton and Saloman (1981)	100–400
Spot	*Leiostomus xanthurus*	Darnell (1958)	40–150
		Schwartz et al. (1980)	60–130
Spotted seatrout	*Cynoscion nebulosus*	Darnell (1958)	40–400
		Carr and Adams (1973)	40–130
Southern flounder	*Paralichthys lethostigma*	Darnell (1958)	100–400
		Powell (1974)	100–400
Striped bass	*Morone saxatilis*	Manooch (1972)	125–714
		Hollis (1952)	NA
Striped mullet	*Mugil cephalus*	Darnell (1958)	97–327
		Odum (1970)	NA
Summer flounder	*Paralichthys dentatus*	Poole (1964)	>250
		Powell (1974)	100–400
		Schwartz et al. (1980)	50–150
Weakfish	*Cynoscion regalis*	Schwartz et al. (1980)	40–140
		Merriner (1975)	Age 0–4
Winter flounder	*Pseudopleuronectes americanus*	Kennedy and Steele (1971)	80–460
		Wells et al. (1973)	NA
		Langton (unpublished)[a]	NA
		Crustaceans	
Blue crab	*Callinectes sapidus*	Darnell (1958)	30–197 (width)
		Tagatz (1968)	30–200 (width)
Brown shrimp	*Penaeus aztecus*	Jones (1973)	25–104
Pink shrimp	*Penaeus duorarum*	Odum (1971)	6–19
White shrimp	*Penaeus setiferus*	Darnell (1958)	91–142
		Molluscs	
Eastern oyster	*Crassostrea virginica*	Galtsoff (1964)	
Northern quahog	*Mercenaria mercenaria*	Walne (1970)	
Softshell	*Mya arenaria*		
Atlantic surfclam	*Spisula solidissima*		

[a] R. W. Langton. Food of nine northwest Atlantic pleuronectiform fishes. National Marine Fisheries Service, Woods Hole, Massachusetts.

cular plants, which are used rather directly as detritus with little loss to intervening microbial degradation.

System Boundaries and Characteristics

The system modeled approximates the zoogeographic "Trans-Atlantic Province" described by Forbes (1856): the coastal zone from approximately 31°N to 41°N. This region is geologically and physiographically homogeneous from north to south. It is a coastal plain covered by Quaternary sediments with low local relief and characterized by mudflats, marshes, barrier islands with sandy beaches, and a shallow continental shelf. Much of the primary production is from extensive stands of emergent vascular plants. In addition to phytoplankton and benthic algae, submerged vascular plants also are common. Sea grass (primarily *Zostera* spp.) is generally confined to areas shallower than 2 m, primarily because of poor light penetration. A high concentration of suspended organic particulates supports a harvest dominated by filter-feeding animals—especially menhaden and bivalve molluscs.

Our model of trophic flows within this coastal system includes 25 species of aquatic animals that contribute substantially to fishery harvests, and their supporting food web (Table 1). These 25 species were lumped into 17 yield categories (Table 2). A few harvested species like dogfish sharks (Squalidae) and whelks (*Busycon* spp.) were excluded from the model because their landings are insignificant (generally <0.1% of the yield). A few others caught within our latitudinal boundaries, such as reef fish and tunas, are not considered part of the system because they occur primarily offshore and presumably derive their energy from a different food web.

Our choice of the spatial dimensions for the model was based on the availability of data, our assumptions about key processes, and the importance of boundaries that capture essential properties of the system and across which few interactions occur. The boundaries include all coastal areas from the southern border of Georgia through New York State and from the freshwater–marine interface out to 8 km offshore. The major habitats included are estuaries, salt marshes, and nearshore coastal waters. Estimates of habitat area and fishery yield are available by state. The latitudinal boundaries encompass most seasonal north–south migrations of fish important to the system. In winter, offshore migration occurs; because of lower temperatures, however, feeding and growth are probably slight beyond our seaward boundary. We assume that net migration is zero and that most of the fishery harvest and food that supports it come from within 8 km of shore. The choice of an 8-km boundary is somewhat arbitrary; however, at least 70% of landings of species harvested in the system are caught within 5 km of shore (NMFS 1957–1974, 1982). Catches decrease rapidly with distance from shore, and we have included only nearshore species. Movement of organic material among included habitats is substantial. No ecological system operates in isolation, and some material also moves in and out of this coastal system by a variety of routes. Importation and exportation rates (e.g., biological movements to or from terrestrial or other aquatic systems, ground- and surface-water fluxes, sedimentation or resuspension, oceanic mixing) generally are variable and poorly documented. For purposes of this analysis, we assume that net transport of organic matter across our boundaries

TABLE 2.—Average yield (1,000s of tonnes dry weight) and the ratio of total mortality (Z) to fishing mortality (F).

Species	Dry weight yield	Z/F Known[a]	Z/F Estimated[b]	Z/F Assigned[c]
Clams and oysters	16.5			2.2
Atlantic menhaden	97.3	1.4		
Striped mullet	0.4			2.2
Penaeid shrimps	2.3	3.0		
Blue crab	12.7	2.6		
Northern puffer	0.6			2.2
Black drum	0.5			2.2
Winter flounder	0.9	2.9		
Atlantic mackerel	0.4			2.2
Spot	1.3			2.2
Atlantic croaker	1.0			2.2
Red drum	0.3			2.2
Summer and southern flounders	2.2	1.4		
Seatrouts	1.6		2.6	
Striped bass	2.2	1.9		
Bluefish	2.5		2.1	
Spanish and king mackerels	1.1		1.8	
Total	143.8			

[a] Sources for known Z/F: Atlantic menhaden: Schaaf and Huntsman (1972); penaeid shrimp: Costello and Allen (1968), McCoy (1968, 1972), and Purvis and McCoy (1974); blue crab: Terry Shoaler, North Carolina Department of Natural Resources, and W. A. Van Engel, Virginia Institute of Marine Science (personal communications); winter flounder: Klein-MacPhee (1978); summer and southern flounders: Chang and Pacheco (1975); striped bass: Setzler et al. (1980).

[b] Sources of estimates of Z/F (Von Bertalanffy growth parameters or catch-curve data): seatrouts: Perlmutter et al. (1956), Taylor (1916), and Merriner (1973); bluefish: Wilk (1977); Spanish mackerel: Berrien and Finan (1977b); king mackerel: Berrien and Finan (1977a).

[c] Arithmetic average of the nine known or estimated ratios.

by all such processes is negligible; our experience suggests this is a reasonable assumption for the production system in question. In any event, decisions of this kind are necessary for analyses of this nature (e.g., Steele 1974).

Data and Sources

In developing the model we summed commercial and recreational yields and determined the amount of primary production required to produce this combined yield based on trophic relationships summarized from dietary studies. We converted the estimates of food needed to produce the yield to estimates of food required for the populations of yield species based on the fraction of their mortality represented by harvest. Summarized information on primary production in the system was used as a means of evaluating the estimates of food required to sustain the yield. Commercial catch data were obtained from *Fishery Statistics of the United States* for the years 1955 through 1974 (NMFS 1957–1974). Recreational catches came from four specially conducted surveys (Clark 1962; Deuel and Clark 1968; Deuel 1973; D. G. Deuel, National Marine Fisheries Service [NMFS], personal communication). Three estimates of bias in these surveys were available. Deuel (1973) cited two surveys that indicated his estimates were high by factors of 3 and 4. G. R. Huntsman (NMFS, personal communication) independently estimated from his headboat surveys that Deuel's statistics were high by a factor of 4. Therefore, we used only one-fourth of the reported recreational landings. All recreational and commercial fish yields (Table 2) are expressed on a dry-weight basis, and are averages for the 20-year period 1955–1974. Lacking landing statistics, we have not considered the recreational harvest of shellfish. The average commercial yield of clams and oysters was 16.5×10^6 kg dry weight. This estimate is based on the assumption that half the shells are not returned to the system (Price et al. 1976), a multiplier of 12.75 (Branch of Statistics, NMFS, Beaufort, North Carolina, personal communication) to convert reported landings (weight of meats) to total live weight, and an additional multiplier of 0.031 to convert live weight to dry weight of meat plus one-half the organic content of shell. The latter factor was an average for eastern oysters and northern quahogs (T. J. Price, NMFS, personal communication).

Information on mortality of yield species that allowed calculation of the ratio of Z (instantaneous rate of total mortality) to F (instantaneous rate of fishing mortality) was obtained for nine species that represent 85% of the yield (Table 2). For six of the species, information was available to calculate the ratio directly. We estimated the ratio for three additional species from information on other life history parameters. We first obtained an estimate of Z from either catch curves or mean age (Ricker 1975); we then estimated M, the instantaneous rate of natural mortality, from a multiple-regression equation involving von Bertalanffy growth parameters K (growth coefficient), and L_∞ (asymptotic maximum length; Pauly 1980); F was obtained by subtraction.

Our description of trophic relationships is a summary of quantitative studies on the diet of yield species (Table 3). Because dietary information is variable, we averaged the results of available studies. Recognizing that animals change diet as they grow, we included available information for all stages from juvenile through adult (Table 1). For most species, the information cited was from dietary breakdowns by percent weight or volume. Such quantitative information is less available for the filter feeders (Atlantic menhaden and molluscs) so our average diets for these species include some information from qualitative descriptions. It is difficult to trace the food chain from yield back to primary producers because the taxonomic description of food items at the lower trophic levels, particularly non-yield invertebrates, is sketchy. We divided food items into six general categories (molluscs, crabs, shrimp, other crustaceans, other omnivores, and other herbivores), basing these categories on taxonomic information and general perceptions of differences in feeding habits. Lumping of some vertebrates into "forage fish" was required because some published data were similarly treated and some items were not identified in greater detail; such lumping also aided the subsequent calculation of ecological flows. The footnotes of Table 3 give all available information on the composition of these lower trophic stages. We present them to indicate the state of knowledge and to permit independent evaluation of whether or not we were cavalier in our description of flow patterns.

Total net primary production for the system was estimated as the sum of organic production by three plant communities: emergent vegetation of tidal marshes, submerged sea grasses, and phytoplankton production. The areas of these three plant communities and their production rates (Table 4) give a total annual net primary production of 25.7×10^{12} g organic matter.

Calculation of Food Chain Flow Rates through Yield Species

Our basic calculations were the cost of organisms (i.e., weight of plants required to produce a given weight of animal). The estimated costs for each species were multiplied by the yield and summed to give the cost of the total harvest. Such cost estimates of producing the yield underestimate the relative importance of fishery species in the food web because they do not include flows through those species to unharvested production. Adjustment to account for this additional cost (which goes to natural mortality of yield species) gives an estimate of the cost of maintaining the fishery populations. We made the adjustment by multiplying the cost of producing the yield by the Z/F ratios from Table 2. As temporal changes in composition and average trophic level of the harvest occur, we show similar changes in estimated costs.

Our estimated cost of producing a yield organism is based on the described food chain leading back to plants (Table 3) and assumed food conversion efficiencies (dry weight gained per dry weight eaten) at each step in the food chain. Both diet and growth (i.e., food conversion) efficiency vary with size or developmental stage of the consumer, environmental conditions, and other factors. We based our calculations on average conditions. The dietary studies (Table 1) included a wide range of fish sizes, locations, seasons, and years, and thus represent an estimated average.

Based on published reviews of laboratory measurements, we assumed an efficiency of 20% for all trophic steps except for the formation of detritus. Winberg (1956) reported a value of 20% for carnivorous fish, and the average for aquatic invertebrates and fishes (Welch 1968) was also about 20%. Brett and Groves (1979) averaged data for young fish feeding well at optimal temperatures and reported 20% for herbivores and 29% for carnivores. The latter values probably overestimate efficiencies that occur in nature because some fish are not young and many probably spend time under suboptimal environmental conditions. Food conversion efficiencies of wild fish defy direct measurement.

The estimated cost of producing a yield organism depends on the animal's growth efficiency, on its diet, and on the growth efficiency and diet of each organism in the food chain back to plants. For example, an animal with a growth efficiency of 0.20 on a plant diet has a cost of 5; if it ate another animal that ate plants and growth efficiency was 0.20 at each step, its cost would be $1/(0.20 \times 0.20)$ or 25. The cost of producing an organism with a mixed diet is an average of the costs of all food items, weighted by the proportion of each component of the diet:

$$C_i = (1/\mathrm{ge}) \sum_j C_j P_j; \qquad (1)$$

C = cost of producing a unit of organism;
ge = growth efficiency;
i = consumer organism;
j = food organism;
P = proportion of an item in diet of consumer organism.

In calculating costs from the top down, we dealt with three types of organisms according to whether their costs were (1) calculated from an observed average diet, (2) calculated from an assumed diet, or (3) assigned for initial calculation according to our best estimates of the likely cost. The 17 yield categories (columns of Table 3) have specified diets from which we calculated the cost according to equation (1). There are seven generalized food categories for which diets were assumed (rows 3–9 in Table 3). Unidentified molluscs, crustaceans, and herbivores were assumed to eat plants; unidentified crabs and shrimp were assumed to eat half plants and half detritus; omnivores were assumed to eat food energetically equivalent to detritus; and squids were assumed to eat forage fish. We calculated the costs for these generalized food categories from equation (1). Plants cost 1, by definition.

The most uncertain links in the food web between yield species and plant production involve detritus and forage fish, two food categories that are not well described in terms of production cost or taxonomic composition. Detritus is plant material that has lost part of its energy, largely through microbial decomposition. For initial calculation, we assumed that detritus consists of one-half unaltered plants and one-half microbes or microbial by-products produced at an efficiency of 0.3. Detritus of this composition would have a cost (C_D) of 1.54, which is equivalent to a 35% energy loss. Although the exact composition of detritus is not known, the 30% efficiency for microbes is likely (Robinson et al. 1982; Benner et al. 1988). Forage fish is the other category with an initially assigned cost (C_{FF}). This category, which includes unidentified species, unspecified proportions of species

TABLE 3.—Average dietary composition of species harvested in coastal waters of the eastern USA from New York through Georgia. The values are percentages of dry weight or volume ingested. Footnotes show the level of specificity presented in papers cited (Table 1).

	Harvested species								
Food category	Clams and oysters	Penaeid shrimps	Blue crab	Atlantic menhaden	Striped mullet	Northern puffer	Black drum	Winter flounder	Summer and southern flounders
Plants	100	18	4	30	37			20	
Detritus		36	6	60	62			7	
Nonyield or unclassified									
Molluscs		7	4			50	66	4	
Crabs			6						
Shrimps									6
Crustaceans		5[c]	11	10		50	12[d]	9	30[e]
Omnivores		35[g]	2[h]		1			28[g]	
Herbivores			12				22	24[i]	3
Squids									
Cannibalized blue crabs			4						
Forage fish			12					8	51[k]
Clams and oysters			39						
Atlantic menhaden									1
Striped mullet									
Penaeid shrimps									1
Blue crabs									2
Winter flounder									5
Atlantic mackerel									
Spot									
Atlantic croaker									
Seatrouts									

[a] 17% pteropods, 2% squids.
[b] Mostly blue crabs.
[c] Copepods and ostracods.
[d] *Rithropanopeus.*
[e] Mostly mysids.
[f] 11% mysids.
[g] Polychaetes.
[h] Annelids.
[i] 20% coelenterates, 2% echinoderms, 2% other.
[j] Appendicularians, chaetognaths, animal remains.
[k] Anchovy, bluefish, seatrout, Atlantic croaker, spot.
[l] Atlantic croaker, spot, anchovies, Atlantic menhaden.
[m] 20% *Fundulus,* 12% *Menidia,* 9% clupeids, 4% anchovies.
[n] 21% other clupeids, 13% anchovies.
[o] 15% anchovies.
[p] 30% clupeids, 25% anchovies, 4% jacks.

with described diets, and others with unknown diets, was assigned a cost of 25. This assignment can be evaluated with the fragmentary information on species composition of this group (footnotes to Table 3) and subsequently calculated costs of yield species (presented in Table 5). We consider both assigned costs to be conservative (i.e., underestimates).

Using equation (1) at successive steps in the food web, we reduced the information in Table 3 to a set of cost equations. For each yield category, the cost of production is a function of the plant production, detritus, and forage fish consumed in that food web (Table 5). For example, with growth efficiencies of 0.2 and a diet from Table 3, the cost of Atlantic menhaden is

$$\begin{aligned} C_{men} &= 5(0.3 \times 1 + 0.6 \times C_D + 0.1 \times 5) \\ &= 4 + 3C_D \\ &= 8.6, \text{ if we assume } C_D = 1.54. \end{aligned}$$

We see that C_{men} cannot be calculated until the cost of unidentified crustaceans is calculated (from their assumed diet). The cost per unit yield (C_i) times the yield (Y_i) equals CY_i, the total amount of primary production required for the yield of each species. The sum of CY_i over all yield species is TCY, the total cost of the system yield. We developed a computer algorithm, using matrix algebra, that calculates C_i, CY_i, and TCY. As structured, TCY depends on the diet matrix (Table 3), the yield vector (harvest by species, Table 2), the assumed growth efficiencies, and the assumed costs of detritus and forage fish. The computer model helped us explore the response (TCY) of the system modeled to variable inputs.

The sum of calculated costs (Table 5) times average yield (Table 2) for all 17 yield categories gives a total cost of the yield. It is over 2.6×10^9 kg organic matter, which is about 10% of the total primary production (Table 4). For simplicity of

TABLE 3.—Extended.

Food category	Harvested species							
	Red drum	Atlantic mackerel	Spot	Atlantic croaker	Bluefish	Striped bass	Seatrouts	Spanish and king mackerels
Plants	2		2	1			1	
Detritus	1		6	5				
Nonyield or unclassified								
Molluscs		18[a]	4	2				
Crabs	29[b]			1				
Shrimps				1				
Crustaceans	9			22	1	1	16[f]	
Omnivores			9[h]	30[h]				
Herbivores	10	31[j]	24	16			4	
Squids					1			6
Cannibalized blue crabs								
Forage fish	28[l]	6	3	14	66[m]	40[n]	54[o]	87[p]
Clams and oysters			14	5				
Atlantic menhaden	1				21	51	6	5
Striped mullet								1
Penaeid shrimps	9			1	3	1	3	
Blue crabs	9			1		1		
Winter flounder								
Atlantic mackerel								1
Spot					6	4		
Atlantic croaker	1						3	
Seatrouts					2	2		

summary we combined costs of the yield into five major categories (Figure 1). About 70% of the total yield is Atlantic menhaden, with a low unit production cost of 9, and 10% is piscivorous fish (red drum, flounders, seatrouts, striped bass, bluefish, mackerels). These piscivores have a high average cost of about 100, and consequently account for slightly more of the total cost than Atlantic menhaden (Figure 1). About 70% of the total cost is required for the yield of menhaden and piscivores. The 20-year average unit cost for all groups (wherein each C_i is weighted by its yield) is only 18 (Figure 1).

In order to examine the effects of variation in magnitude and species composition of the harvest, we calculated average cost for 5-year intervals (Figure 2). As the total yield increased from 120 to 170 × 10^3 tonnes, the percentage of Atlantic menhaden in the yield increased from 55% to 75%. Because Atlantic menhaden have a low cost per unit yield, this increase caused the average cost to decrease from 22 to 16. The net effect was a roughly constant TCY, which increased only 1% as yield increased 40%. The implication of this for fishery exploitation is that, if food is limiting in the system as implied by the nearly constant TCY, total yield from the system can be increased only by increased harvesting of low-cost items and a concomitant reduction in harvest of higher-cost species.

After we adjusted TCY for natural mortality of yield species, our estimate of the cost to produce the yield population (TCP) was 5,211 × 10^9 g organic matter (Table 5), about 20% of the primary production. Because average Z/F of the species weighted by yield is 2.0, the average production cost per unit yield is 36, or twice CY.

System Comparisons

Comparison of summary information from four different continental shelf ecosystems reveals fundamental differences (Table 6). The ecosystem on the east coast of the USA that we describe in this paper is most similar to that in Louisiana. These two areas have similar levels of primary production per unit area (PP/A), including important contributions by vascular plants, as well as similar species and fisheries. The main difference is that the Louisiana system exports a substantial amount of primary production, which is thus unavailable

TABLE 4.—Net primary production of organic matter in coastal areas of the eastern USA from New York through Georgia.

Producer	Area (in 10^9 m^2)	Production rate $g/(m^2 \cdot year)$	Yearly production (in 10^{12} g organic matter)
Emergent marsh plants	8.26[a]	1,200[b]	9.9
Sea grass	1.3[c]	600[d]	0.8
Phytoplankton and benthic algae	43.0[e]	350[f,g]	15.0
Total production			25.7

[a] Unpublished inventory (Ralph Tinner, U.S. Fish and Wildlife Service, personal communication).
[b] Mean of 19 independent estimates between 31 and 39°N (Stiven and Plotecia 1976).
[c] Area to water depths of 2 m (Spinner 1969); sea grass is usually limited to these depths and occurs from North Carolina to New York (Polly Penhale, National Science Foundation, Washington, D.C., personal communication).
[d] Thayer et al. (1975); Polly Penhale (personal communication).
[e] 3.0×10^{10} m^2 within headlands (Spinner 1969). 1.3×10^{10} m^2 from headlands to 8 km based on coastal distance of 1,635 km (Shalowitz 1964).
[f] The carbon fixation rate, 175 $g/(m^2 \cdot year)$, is the average from 12 studies, 10 from New York to North Carolina (Smayda 1973) and 2 from Georgia (Turner et al. 1979; Haines 1979). We assume organic matter production is twice the carbon fixation (Ryther 1956).
[g] In shallow estuarine areas, phytoplankton production is often lower (Ferguson et al. 1980), but it is supplemented by benthic algae. We assume that total algae production in shallow water is the same as phytoplankton production in deeper areas.

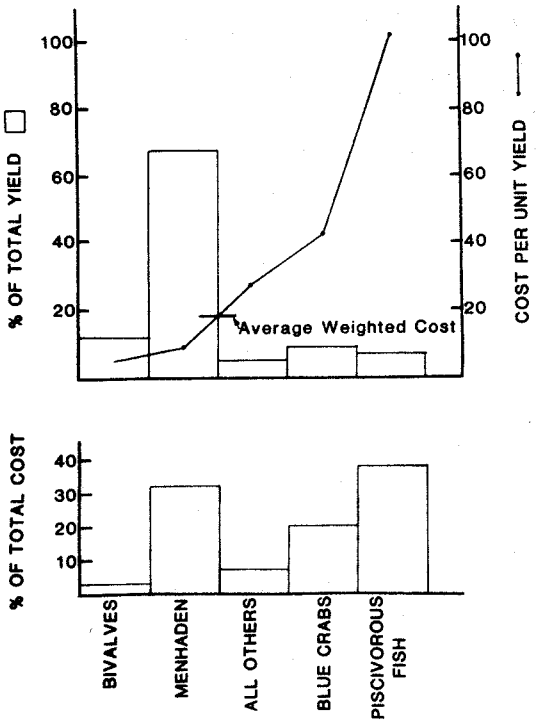

FIGURE 1.—Average composition of yield and its cost of production in the Atlantic coastal sector, New York–Georgia, 1955–1974. Cost, calculated on a dry-weight basis, is the units of primary production necessary to produce a unit of yield.

for fish production and results in a lower yield per unit area (Bahr et al. 1982).

Based on plant production (PP/A) in the North Sea, we might expect yield per unit area (Y/A) to be low. However, less primary production is needed to produce a unit of harvest (PP/Y) than in the other systems. Thus, Y/A is higher than might be expected based only on consideration of phytoplankton production. The low PP/Y in the North Sea might reflect a more efficient food chain or a more intensive harvesting of the biota. Given no reason to expect that North Sea food chains are more efficient, we suspect greater harvesting intensity.

The summary information from Georges Bank is not easy to reconcile. Primary production is much higher than in the other systems but so is the bioenergetic cost of producing the harvest (PP/Y). This cost may be even higher than indicated because of possible bias in the reported yield (Y/A = 2.1). Based on an estimated fish production of 1.9 (Grosslein et al. 1980) and a natural mortality equal to the fishing mortality, we would expect a Y/A of only 0.95. The difference between observed (2.1) and estimated fishery yield (0.95) may indicate a boundary problem, i.e., some of the harvest attributed to Georges Bank may be produced elsewhere. Regardless of which yield estimate is used, the ratio PP/Y is much higher than in the other systems.

The yield and primary production of the systems (Table 6) indicate levels of exploitation, but provide little information on the systems' capabilities to support greater harvests. If unutilized food chains exist (along the Atlantic coast these might include flows to sharks, marine mammals, seabirds, and turtles), primary production used by such chains is unavailable to support fishery yield, and the fraction of organic matter production unrelated to fishery yield is a measure of underexploitation. Our knowledge of fishery systems includes little or no information about unutilized

TABLE 5.—Cost equations based on average diets from Table 3, estimated cost of production (C_i), amount of primary production needed to produce average yield (CY_i) and the amount needed to sustain the yield populations (CP_i). C is units of organic matter/unit yield, C_D is cost of detritus, and C_{FF} is cost of forage fish. CY and CP are in 1,000s of tonnes organic matter. It is assumed that $C_D = 1.54$ and $C_{FF} = 25$.

Taxa	Cost equations C_i =	C_i	CY_i	CP_i
Clams and oysters	5	5	82	180
Atlantic menhaden	$4 + 3\,C_D$	9	839	1,174
Striped mullet	$1.85 + 3.35\,C_D$	7	3	6
Penaeid shrimps	$3.9 + 10.55\,C_D$	20	46	139
Blue crab	$20.94 + 1.86\,C_D + 0.72\,C_{FF}$	42	530	1,380
Puffers	25	25	15	33
Black drum	25	25	13	28
Winter flounder	$10.25 + 7.35\,C_D + 0.4\,C_{FF}$	32	28	82
Atlantic mackerel	$23.5 + 0.3\,C_{FF}$	31	12	27
Spot	$20.1 + 2.55\,C_D + 0.15\,C_{FF}$	28	36	79
Atlantic croaker	$12.8 + 8.62\,C_D + 0.74\,C_{FF}$	45	45	98
Red drum	$19.62 + 10.97\,C_D + 1.76\,C_{FF}$	81	24	53
Summer and southern flounders	$14.05 + 3.45\,C_D + 2.72\,C_{FF}$	87	192	269
Seatrouts	$10.25 + 5.28\,C_D + 2.81\,C_{FF}$	89	142	369
Striped bass	$16.74 + 9.31\,C_D + 2.35\,C_{FF}$	90	198	375
Bluefish	$12.09 + 6.02\,C_D + 3.88\,C_{FF}$	118	296	621
Spanish and king mackerels	$2.27 + 0.92\,C_D + 5.87\,C_{FF}$	150	165	298
Total			2,667	5,211

food chains, which often leads to the tacit assumption that none exist. Our description of trophic flows in the coastal waters of the eastern USA provides no direct assessment of primary production that does not lead to yield. However, we do have a minimum estimate of flows to yield species (20% of total primary production). If our description of the fishery food chains is accurate, the remaining 80% of primary production is consumed in chains independent of our yield and might contribute additional yield. However, the extent to which any of this excess production is consumed in our yield chains is the extent to which we have underestimated cost and overestimated the production that could contribute to additional yield. For the other systems summarized in Table 6, we have no estimate of the primary production that could contribute to additional yield because the food chains were specified in such a way that primary production was balanced by fish production.

Food Chain Constraints

For the U.S. Atlantic coast, our estimates of average production cost (36) and fraction of primary production used by species in food chains leading to yield, 0.20, are low because we were consistently conservative wherever we made assumptions regarding diets or unknown costs of food items. The amount by which these estimates are low depends on how much we underestimated

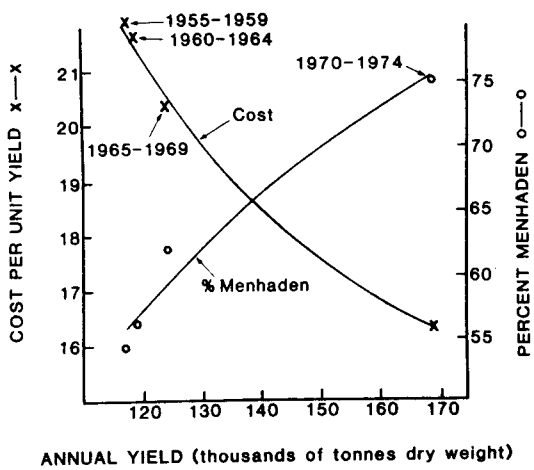

FIGURE 2.—Weighted average cost per unit yield for all species along the U.S. Atlantic coast, and percent contribution of Atlantic menhaden to the yield, as functions of average annual yield during 5-year periods from 1955 to 1974.

TABLE 6.—Summary characteristics of four major fishery production systems. Area (A) is expressed as 10^{10} m^2, net primary production (PP) is grams organic matter, and yield (Y) is grams dry weight.

Statistic	East coast USA	Louisiana[a]	North Sea	Georges Bank
A	5.3	11	57[b]	5.3[b]
PP/A	500	600 or 240[c]	180[d]	900[g]
Y/A	2.7	1.4	1.3[e]	2.1[h]
PP/Y	179	170[c]	140[f]	370[i] or 430[j]

[a] Bahr et al. (1982).
[b] Grosslein et al. (1980).
[c] Calculated from nonexported organic matter on the basis of 18.8 kJ/g.
[d] Calculated from Steele (1974) on the basis of 2 g organic matter per gram carbon.
[e] Calculated as the ratio of PP/A to PP/Y.
[f] Based on kcal/m^2 (Steele 1974: Figure 2.7).
[g] Cohen et al. (1982), on the basis of 2 g organic matter per gram carbon.
[h] Calculated from landings (ICNAF 1969–1978) on the basis of dry weight = 0.25 live weight.
[i] Based on Edwards and Kirkley (1983: Figure 1).
[j] Calculated as the ratio of PP/A to Y/A.

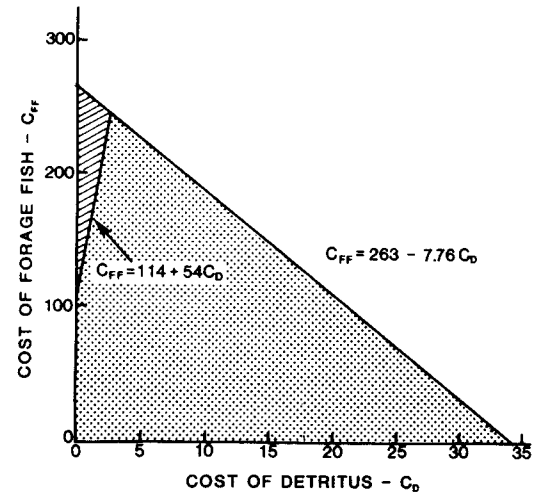

FIGURE 3.—Parameter space for unit cost of producing forage fish (C_{FF}) and detrital cost (C_D). Stippled plus cross-hatched area is the region where total cost of yield does not exceed total primary production when C_{FF} is independent of C_D. Cross-hatched area represents feasible combinations when C_{FF} is the linear function of C_D (text equations 4 and 6).

C_D, the cost of consumed detritus. We know they will also be low unless and until we account for the total cost of producing all forage fish and not just those that are consumed by our yield species.

The range of possible values for C_D and C_{FF} can be determined from other information. In our model with a fixed diet matrix and fixed vectors of growth efficiencies and yield, the average cost of yield is a linear function of C_D and C_{FF}:

$$CY = 6.64 + 2.88C_D + 0.30C_{FF}. \quad (2)$$

This equation is the average of cost equations for all yield categories (Table 5) weighted by yield. The average for all yield categories when weighted by both yield and Z/F is the cost of producing an average unit of yield:

$$CP = 13.05 + 4.89C_D + 0.63C_{FF}. \quad (3)$$

If all energy in the system is used in the described trophic structure (Table 3), CP = 179 (Table 6) and we can show the feasible parameter space for C_D and C_{FF} (Figure 3). Substituting 179 for CP in equation (3) and rearranging the terms, we obtain equation

$$C_{FF} = 263.41 - 7.76C_D. \quad (4)$$

This equation, with a negative slope and intercepts of 263 and 34, represents all possible combinations of C_{FF} and C_D in which all primary production in the system is accounted for (i.e., CP calculated from equation 3 equals 179). Any combination of values above that line is inadmissible because the net primary production would be insufficient for the secondary production required by the exploited system (CP > 179). If C_D and C_{FF} vary independently, any pair is feasible that falls below this line (CP < 179).

Equation (4) considerably restricts the feasible values of C_D and C_{FF}; however, it is unlikely that they vary independently. We know from the diet matrix, as summarized by equation (2), that the cost of yield species does not vary independently of C_D. Also, we know from Table 1 that some of the forage fish consumed are yield species. If the species suite comprising forage fish (FF) is trophically similarly to the mix of harvested species (minus clams and oysters), we can assign the average unit cost, $C_{FF} = 6.85 + 3.25C_D + 0.34C_{FF}$ (the weighted average cost per unit yield of 16 equations in Table 5). Solving for C_{FF} as a function of C_D we obtain

$$C_{FF} = 10.38 + 4.92C_D. \quad (5)$$

This is a conservatively low estimate, because it is heavily weighted by the cost of Atlantic menhaden, which are at a lower trophic level than

other available finfish. If $C_D = 1.54$, as assumed, C_{FF} would equal 18 rather than the value of 25 we used in our basic model computations. However, equation (5) only accounts for the cost of forage fish that are consumed.

Because the forage fish that are ingested are only a part of larger populations, a more reasonable estimate of the cost of producing the yield would include the cost of producing those forage fish populations. For this we need an estimate of the predation rate on forage fish (i.e., the fraction of total natural mortality that is consumed by our yield species). The only estimate available can be obtained from the yield of finfish. We know from Table 2 that the natural mortality of the 16 groups of recruited finfish ($Y \times [(Z/F) - 1]$) is 153×10^6 kg/year. The amount of this mortality that is due to consumption in the identified food chains (Table 3), based on average yield (Table 2), is 13.2×10^6 kg/year. The ratio of total natural mortality (153) to the amount consumed by the yield food chains (13.2) is about 11. This ratio is an estimate of the production of yield species per unit consumed; it may be biased. The numerator may underestimate mortality (prerecruits are not included), hence the ratio may be underestimated. The denominator may not include, among unidentified forage fish, all of the yield species actually consumed, thereby giving an overestimated ratio. We assumed, however, the same ratio for forage fish; multiplying equation (5) by 11 gives

$$C_{FF} = 114 + 54C_D, \qquad (6)$$

the equation for the line in Figure 3 with the positive slope, which we assume to represent a minimal cost for producing the forage fish. Now the feasible parameter space is restricted even more, to the upper left triangle. The intersection of the lines on Figure 3 is at $C_D = 2.4$ (by solution of the simultaneous equations 4 and 6), which is the maximum permissible value for C_D. Its value represents an extremely efficient transfer from plant production to the detritus consumed by animals in the described food chains. From equation (1) with $C_D = 2.4$ and the cost of plant production equal to 1, the efficiency of detritus production is 0.42. Thus, no more than 58% of the energy contained in plants that become detritus can be dissipated before reaching the documented food chains.

Choosing the lowest possible value for C_D ($C_D = 1$), we can determine the minimum fraction of primary production in the system for which this model accounts. Substituting equation (6) into equation (3) gives the average cost of production (CP^*) in terms of C_D:

$$CP^* = 84.87 + 38.91C_D. \qquad (7)$$

Because C_D can range from 1 to 2.4, CP^* can vary from 124 to 179. Thus, depending on the efficiency of detrital production, the model accounts for between 69 and 100% of the total primary production within the boundaries of the system (Table 6). Furthermore, we can conclude that algal production alone, which is 58% of the total primary production, is insufficient to support the system. At least 11% of the total net primary production consumed by the yield system must come from vascular plants (i.e., at least 26% of vascular plant production must enter the yield system). As C_D goes up, of course, more vascular plant production is required to drive the system. For example, at a cost of 2.4, 42% of the total primary production used must come from vascular plants. This equals the total marsh and sea grass production.

By closely examining many aspects of the biology of the yield species, we have learned enough to offer some provocative hypotheses regarding system functioning.

- No more than 58% of primary production that goes through the detrital compartment can be trophically dissipated before being consumed by described fishery food chains.
- The coastal system described requires an organic matter subsidy of no less than 26% of marsh and sea grass production.

The reliability of these estimates is contingent on the validity of the data and assumptions described. Although one might argue with our many choices on these matters, our major concern is the need to specify an outer boundary with no net flux across it. Our designation (8 km from shore) is based on general information about the location of fishery harvest, but just where the boundary should be placed and how porous it will be at that location are not amenable to precise delineation. Its seaward displacement would increase the yield minimally because most of the harvest is taken close to shore; however, such displacement could greatly increase the area and thus our estimate of algal production. Based on a constant yield but an increasing amount of algal production, the relative importance of vascular plant material declines as the outer boundary is moved seaward. The

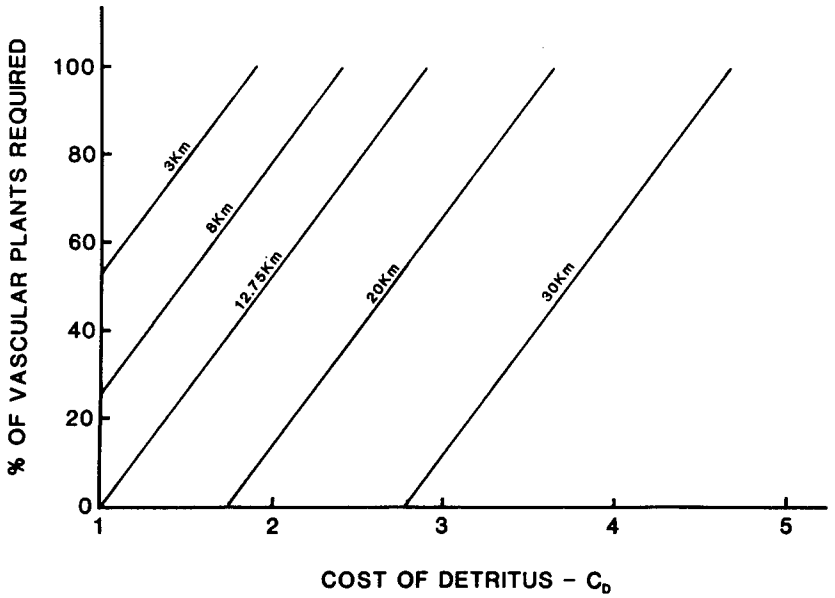

FIGURE 4.—Fraction of vascular plant production that is required to sustain the fishery yield as functions of the system's outer boundary location in kilometers (km) from shore and cost of detritus consumed (C_D).

boundary must be at least 3 km from shore because the algae consumed by the yield system (equation 7 times average yield) is equivalent to all the algae produced within that boundary. With boundaries more seaward, our estimate of the fraction of vascular plant material needed to produce the total yield depends on C_D (Figure 4). When the boundary is less than 12.75 km from shore, total algal production will be inadequate to provide the algae and detritus consumed even with $C_D = 1$. With primary production at a level equivalent to an outer boundary of 30 km, we do not need any vascular plant production if $C_D < 2.8$; however, with $C_D = 4.7$, we need all of it.

Summary

This model has sharply focused on our major areas of ignorance. We need to know what detritus is and what happens to it before it gets eaten by a "fish" (C_D). We need to know what species are forage fish, and what they eat (C_{FF}). In order to relate fishery production to total ecosystem operation, we also need better estimates of natural mortality rates, especially for forage fish and prerecruits of yield species.

Our understanding of marine ecosystems can be greatly improved by combining data from intensive fisheries with ecological information through top-down modeling. We believe that when other fishery systems are appropriately summarized and compared, the utility of this approach will be more readily appreciated.

References

Bahr, L. M., J. W. Day, and J. H. Stone. 1982. Energy cost accounting of Louisiana fishery production. Estuaries 5:209–215.

Bass, R. J., and J. W. Avault. 1975. Food habits, length–weight relationship, condition factor and growth of juvenile red drum, *Sciaenops ocellata*, in Louisiana. Transactions of the American Fisheries Society 104: 35–45.

Benner, R., J. Lay, E. Knees, and R. E. Hodson. 1988. Carbon conversion efficiency for bacterial growth on lignocellulose: implications for detritus-based food webs. Limnology and Oceanography 33:1514–1526.

Berrien, P., and D. Finan. 1977a. Biological and fisheries data on king mackerel, *Scomberomorus cavalla* (Cuvier). U.S. National Marine Fisheries Service, Northeast Fisheries Center, Sandy Hook Laboratory, Technical Series Report 8, Sandy Hook, New Jersey.

Berrien, P., and D. Finan. 1977b. Biological and fisheries data on Spanish mackerel, *Scomberomorus maculatus* (Mitchill). U.S. National Marine Fisheries Service, Northeast Fisheries Center, Sandy

Hook Laboratory, Technical Series Report 9, Sandy Hook, New Jersey.

Boothby, R. N., and J. W. Avault. 1971. Food habits, length–weight relationship and condition factor of the red drum, *Sciaenops ocellata*, in southeastern Louisiana. Transactions of the American Fisheries Society 100:290–295.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. Pages 279–352 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8. Academic Press, New York.

Carr, W. E. S., and C. A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Transactions of the American Fisheries Society 102: 511–540.

Chang, S., and A. L. Pacheco. 1975. An evaluation of the summer flounder population in subarea 5 and statistical area 6. International Commission for the Northwest Atlantic Fisheries, Research Document 75/69, Serial 3553, Dartmouth, Nova Scotia.

Clark, J. R. 1962. The 1960 salt-water angling survey. U.S. Fish and Wildlife Service Circular 153.

Cohen, E. B., M. D. Grosslein, M. P. Sissenwine, F. Steimle, and W. R. Wright. 1982. Energy budget of Georges Bank. Canadian Special Publication of Fisheries and Aquatic Sciences 59:95–107.

Costello, T. J., and D. M. Allen. 1968. Mortality rates in populations of pink shrimp, *Penaeus duorarum*, on the Sanibel and Tortugas grounds, Florida. U.S. Fish and Wildlife Service Fishery Bulletin 66:491–501.

Darnell, R. M. 1958. Food habits of fishes and invertebrates of Lake Pontchartrain. Publications of the Institute of Marine Science, University of Texas 5: 352–416.

Darnell, R. M. 1964. Organic detritus in relation to secondary production in aquatic communities. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 15:462–472.

Deuel, D. G. 1973. 1970 saltwater angling survey. U.S. Fish and Wildlife Service Current Fisheries Statistics 6200.

Deuel, D. G., and J. R. Clark. 1968. The 1965 saltwater angling survey. U.S. Bureau of Sport Fisheries and Wildlife Resource Publication 67.

Edwards, R. L., and R. E. Bowman. 1979. Food consumed by continental shelf fishes. Pages 388–409 *in* H. Clepper, editor. Predator–prey systems in fishery management. Sport Fishing Institute, Washington, D.C.

Edwards, R. L., and J. E. Kirkley. 1983. Comments on modeling from the standpoint of a research administrator. Pages 21–33 *in* K. W. Turgeon, editor. Marine ecosystem modeling. U.S. Department of Commerce, Washington, D.C.

Ferguson, R. L., G. W. Thayer, and T. R. Rice. 1980. Marine primary producers. Pages 9–69 *in* F. J. Vernberg and W. Vernberg, editors. Functional adaptation of marine organisms. Academic Press, New York.

Forbes, E. 1856. Map of the distribution of marine life. Plate 31 *in* K. Johnston. The physical atlas of natural phenomena, new edition. W. and A. K. Johnson, London.

Galtsoff, P. S. 1964. The American oyster, *Crassostrea virginica* Gmelin. U.S. Fish and Wildlife Service Fishery Bulletin 64:1–480.

Grant, G. C. 1962. Predation of bluefish on young Atlantic menhaden in Indian River, Delaware. Chesapeake Science 3:45–46.

Grosslein, M. D., R. W. Langton, and M. P. Sissenwine. 1980. Recent fluctuations in pelagic fish stocks of the northwest Atlantic Georges Bank region, in relation to species interactions. Rapports et Procès-Verbaux des Réunions, Conseil Internationale pour l'Exploration de la Mer 177:374–404.

Haines, E. B. 1979. Interactions between Georgia salt marshes and coastal waters: a changing paradigm. Pages 35–46 *in* R. J. Livingston, editor. Ecological processes in coastal and marine systems. Plenum, New York.

Hansen, D. J. 1969. Food, growth, migration, reproduction, and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida, 1963–65. U.S. Fish and Wildlife Service Fishery Bulletin 68:135–146.

Hollis, E. H. 1952. Variations in the feeding habits of the striped bass, *Roccus saxatilis* (Walbaum), in the Chesapeake Bay. Bulletin of the Bingham Oceanographic Collection, Yale University 14:111–131.

ICNAF (International Commission for the Northwest Atlantic Fisheries). 1969–1978. Statistical bulletins 17–28. ICNAF, Dartmouth, Nova Scotia.

Jeffries, H. P. 1975. Diets of juvenile Atlantic menhaden (*Brevoortia tyrannus*) in three estuarine habitats as determined from fatty acid composition of gut contents. Journal of the Fisheries Research Board of Canada 32:587–592.

Jones, R. R. 1973. Utilization of Louisiana estuarine sediments as a source of nutrition for the brown shrimp, *Penaeus aztecus*. Doctoral dissertation. Louisiana State University, Baton Rouge.

June, F. C., and F. T. Carlson. 1971. Food of young Atlantic menhaden, *Brevoortia tyrannus*, in relation to metamorphosis. U.S. Fish and Wildlife Service Fishery Bulletin 68:493–512.

Kennedy, V. S., and D. H. Steele. 1971. The winter flounder (*Pseudopleuronectes americanus*) in Long Pond, Conception Bay, Newfoundland. Journal of the Fisheries Research Board of Canada 28:1153–1165.

Kerr, S. R. 1982. The role of external analysis in fisheries science. Transactions of the American Fisheries Society 111:165–170.

Klein-MacPhee, G. 1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) Circular 414.

Lassiter, R. R. 1962. Life history aspects of the blue-

fish, *Pomatomus saltatrix* (Linnaeus), from the coast of North Carolina. Master's thesis. North Carolina State University, Raleigh.

Lewis, V. P., and D. S. Peters. 1984. Menhaden—a single step from vascular plant to fishery harvest. Journal of Experimental Marine Biology and Ecology 84:95–100.

Linton, E. 1905. Parasites of fishes of Beaufort, North Carolina. U.S. Bureau of Fisheries Bulletin 24:321–428.

Manooch, C. S. 1972. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum) from Albemarle Sound, North Carolina. Master's thesis. North Carolina State University, Raleigh.

McCoy, E. G. 1968. Migration, growth and mortality of North Carolina pink and brown penaeid shrimps. North Carolina Division of Commercial and Sport Fisheries, Special Scientific Report 15, Raleigh.

McCoy, E. G. 1972. Dynamics of North Carolina commercial shrimp populations. North Carolina Division of Commercial and Sport Fisheries, Special Scientific Report 21, Raleigh.

Merriner, J. V. 1973. Assessment of the weakfish resource, a suggested management plan, and aspects of life history in North Carolina. Doctoral dissertation. North Carolina State University, Raleigh.

Merriner, J. V. 1975. Food habits of the weakfish, *Cynoscion regalis,* in North Carolina waters. Chesapeake Science 16:74–76.

Mid-Atlantic Fishery Management Council. 1978. Final environmental impact statement and fishery management plan for the Atlantic mackerel fishery. Mid-Atlantic Fishery Management Council, South Atlantic Fishery Management Council and National Marine Fisheries Service, Dover, Delaware.

Mulkana, M. S. 1966. The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Research Reports 2:97–168.

Naughton, S. P., and C. H. Saloman. 1981. Stomach contents of juvenile king mackerel (*Scomberomorus cavalla*) and Spanish mackerel (*S. maculatus*). Northeast Gulf Science 5:71–74.

NMFS (National Marine Fisheries Service, successor to Bureau of Commercial Fisheries). 1957–1974. Fishery statistics of the United States, 1955–1974. U.S. National Marine Fisheries Service [Bureau of Commercial Fisheries] Statistical Digests 41–68.

NMFS (National Marine Fisheries Service). 1982. Fisheries of the United States, 1981. U.S. National Marine Fisheries Service Current Fishery Statistics 8200.

Odum, W. E. 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus.* Pages 222–240 *in* J. H. Steele, editor. Marine food chains. University of California Press, Berkeley.

Odum, W. E. 1971. Pathways of energy flow in a south Florida estuary. University of Miami Sea Grant Program, Sea Grant Technical Bulletin 7. .

Pauly, D. 1980. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality, and stock recruitment relationships. Pages 154–172 *in* S. Saila and P. Roedel, editors. Proceedings of the workshop on tropical small-scale fishery stock assessment. International Center for Marine Resource Development, University of Rhode Island, Narragansett.

Perlmutter, A. W., W. S. Miller, and J. C. Poole. 1956. The weakfish (*Cynoscion regalis*) in New York waters. New York Fish and Game Journal 3:1–43.

Poole, J. C. 1964. Feeding habits of the summer flounder in Great South Bay. New York Fish and Game Journal 11:28–34.

Powell, A. B. 1974. Biology of the summer flounder, *Paralichthys dentatus,* in Pamlico Sound and adjacent waters, with comments on *P. lethostigma* and *P. albigutta.* Master's thesis. University of North Carolina, Chapel Hill.

Price, T. J., G. W. Thayer, M. W. LaCroix, and G. P. Montgomery. 1976. The organic content of shells and soft tissues of selected estuarine gastropods and pelecypods. Proceedings National Shellfisheries Association 65:26–31.

Purvis, C. E., and E. G. McCoy. 1974. Population dynamics of brown shrimp in Pamlico Sound. North Carolina Division of Commercial and Sport Fisheries, Special Scientific Report 25, Raleigh.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Rigler, F. H. 1982. The relationship between fisheries management and limnology. Transactions of the American Fisheries Society 111:121–132.

Robinson, J. D., K. H. Mann, and J. A. Novitsky. 1982. Conversion of the particulate fraction of seaweed detritus to bacterial biomass. Limnology and Oceanography 27:1072–1079.

Ryther, J. H. 1956. The measurement of primary production. Limnology and Oceanography 1:72–84.

Saloman, C. H., and S. P. Naughton. 1983. Food of king mackerel, *Scomberomorus cavalla,* from the southeastern United States including the Gulf of Mexico. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum NMFS (National Marine Fisheries Service) SEFC (Southeast Fisheries Center) 126, Miami.

Schaaf, W. E., and G. R. Huntsman. 1972. Effects of fishing on the Atlantic menhaden stock: 1955–1969. Transactions of the American Fisheries Society 101: 290–297.

Schwartz, F. J., S. Morgan, M. McAdams, K. Sandoy, and D. Mason. 1980. Food analysis of selected fishes captured in Cape Fear Estuary and adjacent Atlantic Ocean, North Carolina, 1973–1978. University of North Carolina, Institute of Marine Sciences, Morehead City.

Setzler, E. M., and eight coauthors. 1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) Circular 433.

Shalowitz, A. L. 1964. Shoreline of the United States.

Pages 479–484 *in* A. L. Shalowitz, editor. Shore and sea boundaries, volume 2. U.S. Department of Commerce, Coast and Geodetic Survey, Publication 10-1, Washington, D.C.

Shipp, R. L., and R. W. Yerger. 1969. Status, characters and distribution of the northern and southern puffers of the genus *Sphoeroides*. Copeia 1969:425–433.

Smayda, T. J. 1973. A survey of phytoplankton dynamics in the coastal waters from Cape Hatteras to Nantucket. University of Rhode Island, Marine Publication Series 2:3-1 to 3-100.

Spinner, G. P. 1969. The wildlife wetlands and shellfish areas of the Atlantic coastal zone. American Geographical Society, Serial Atlas of the Marine Environment 18, New York.

Steele, J. H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge, Massachusetts.

Stiven, A. E., and R. K. Plotecia. 1976. Salt marsh productivity estimates for North Carolina coastal counties: projections from a regression model. University of North Carolina Sea Grant College, Publication UNC-76-06, Chapel Hill.

Tagatz, M. E. 1968. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. U.S. Fish and Wildlife Service Fishery Bulletin 67:17–33.

Taylor, H. F. 1916. The structure and growth of the scales of the squeteague and the pigfish as indicative of life history. U.S. Bureau of Fisheries Bulletin 34: 285–330.

Thayer, G. W., S. M. Adams, and M. W. LaCroix. 1975. Structural and functional aspects of a recently established *Zostera marina* community. Estuarine research 1:518–540.

Turner, R. E., S. W. Woo, and H. R. Jitts. 1979. Phytoplankton production in a turbid, temperate salt marsh estuary. Estuarine and Coastal Marine Science 9:603–613.

Walne, P. R. 1970. Studies on the food value of nineteen genera of algae to juvenile bivalves of the genera *Ostrea, Crassostrea, Mercenaria* and *Mytilus*. Great Britain Ministry of Agriculture, Fisheries and Food, Fishery Investigations Series II, Marine Fisheries 26:1–61.

Welch, H. E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology 49:755–759.

Wells, B., D. H. Steele, and A. V. Tyler. 1973. Intertidal feeding of winter flounders (*Pseudopleuronectes americanus*) in the Bay of Fundy. Journal of the Fisheries Research Board of Canada 30:1374–1378.

Wilk, S. J. 1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). U.S. National Marine Fisheries Service, Northeast Fisheries Center, Sandy Hook Laboratory, Technical Series Report 11, Sandy Hook, New Jersey.

Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Fisheries Research Board of Canada, Translation 194, Ottawa.

Received September 28, 1989
Accepted February 3, 1991