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Recent Trends in Estuarine Fisheries: Predictions of Fish Production and Yield[1]

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ABSTRACT: Trends in global and United States fish catches were examined to determine the status of estuarine fisheries yields relative to those from other ecosystems. Potential marine fish production, based upon primary production relationships, was estimated globally and for specific marine ecosystems, including estuaries. While global fish catches increased substantially during the past two decades and continued to increase through 1989, catches of estuarine-dependent species have peaked or stabilized. In the United States, total catches have increased but many estuarine-dependent fisheries have declined, although the declines in catches are no more dramatic than those of heavily-fished continental shelf species. Overfishing probably is the primary cause of declines in estuarine and shelf fisheries. A few estuarine-dependent species of the United States have experienced substantial increases in harvests since 1970, for example, Pacific salmons, menhaden, and penaeid shrimps. The percentage contribution of major estuarine fisheries to the United States commercial catch declined between 1970 and 1990, although the yield of these species increased substantially. Global marine fisheries production at trophic level 2.5 was estimated to be 1,359 million tons. Potential yield was estimated to be 307 million tons, but the 1989 world marine catch was only 86.5 million tons. The major fraction, 196 million tons, of the estimated potential yield was for the open ocean where technological constraints may prevent its full realization. Of the remaining 111 million tons of the potential, 18.0 million tons (16.2%) may come from estuaries and probably already is fully exploited. The potential catches from shelves, 68.5 million tons (61.6%), and upwelling areas, 24.8 million tons (22.2%), while considerably larger than those from estuaries, are lower in a relative sense (per unit area) than fisheries production and potential catch in estuarine zones. Relationships between fish production, fish harvest, and primary production were examined in specific estuaries. The developing role of aquaculture and its effect on estuarine fisheries are discussed.

Introduction

High yields of fish from estuaries are a consequence of high primary production levels, the availability of nutrients to sustain productivity, and, in no small sense, the proximity of estuaries and their harvestable resources to fishing ports. It is widely recognized that estuaries serve not only as fishing grounds but also serve as nursery areas for fishery resources that may be exploited there or in coastal fisheries later in life. A fraction exceeding 50% of the total United States' fishery harvests is estuarine or estuarine-dependent in at least some life stages. That fraction is considerably higher in some regions, such as the Gulf of Mexico, where estuarine-dependent resources dominate the catches (Gunter 1967; McHugh 1967).

Fisheries increasingly must compete with other commercial and recreational users, and sometimes abusers, of the estuary. The proximity of cities and ports to estuaries, while facilitating exploitation of resources, also threatens the viability of estuarine production systems. Alteration or loss of habitat and discharge of contaminants are primary concerns. No less serious are effects of excess nutrient loading that may alter the nature or change the level of productivity, may cause seasonal oxygen deficits and may change the community structure of estuarine living resources. Global change and the possibility of rising sea levels that could have major effects on estuarine fish production and the harvesting industries (Kennedy 1990; Morris et al. 1990; Bigford 1991) are a recent and growing concern. Overfishing of highly vulnerable, nearshore vertebrate and invertebrate resources is a pervasive problem (National Oceanic and Atmospheric

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Administration 1991) that too often is not addressed successfully by management and which reduces the long-term yield potential of the resources. The overfishing problem in the coastal ocean is compounded by the inadvertent catch of nontargeted species, the so-called "bycatch." Although generally unevaluated, effects of bycatch must significantly impact ecosystem function by altering trophic relationships and reducing sustainable levels of yields in multispecies fisheries (Murawski 1991).

McHugh (1967), Haedrich (1983), and Dando (1984) have reviewed many of the life history characteristics of estuarine fishes, noting particularly the incidence of anadromy, the propensity for estuaries to serve as juvenile nurseries and the importance of trophic relationships. The relationships between freshwater inputs, nutrient loading, and fish production (usually indexed as harvest) have been demonstrated to be important, and the "agricultural model," in which increasing nutrient loads lead to increased primary production and fish harvests, does seem to apply to estuarine and marine systems (Nixon et al. 1986; Nixon 1992). Increases in river discharges (Aleem 1972; Deegan et al. 1986) and vegetation cover (Turner 1977) are directly related to estuarine-dependent fish harvests. Complex trophic relationships are important in determining harvest levels of coastal marine fishes (Peters and Schaaf 1991), although the roles of many factors, particularly detritus and the cost of forage fish production, remain little understood. Causes of fluctuations in abundances via recruitment variability and in levels of population biomass, a focus of intensive research in the 1970s and 1980s, are poorly understood in estuarine and other aquatic ecosystems.

In this paper, our overall objective is to examine status and trends in recent marine and estuarine fish harvests on a worldwide basis and then specifically in the United States, particularly since 1970. We then review what is known of estuarine productivity and its probable relationship to fisheries yields. Finally, presuming that the "agricultural model" applies, and adopting relationships derived by Nixon (1988) and Iverson (1990), we estimate the levels of global estuarine fisheries production and harvest, and compare them to estimates for other marine ecosystems.

Methods

Catch Statistics

Catch statistics for world fisheries were obtained from summarized information on catches and landings, published annually by the United Nations' Food and Agriculture Organization (1955 to 1991). Total harvests of animal-origin fishery products, both fresh water and marine, excluding mammals but including aquaculture harvests, were obtained. Trends in catches of selected estuarine and nonestuarine species or species groups were examined. Catches were summarized since 1940 for some fisheries but, for most groups, our records begin in 1950 or 1960. The United Nations Food and Agriculture Organization's catch statistics do not report fishing effort and, consequently, do not necessarily indicate the status or trends in stock abundances, although in many cases, inferences about stock status can be made.

Catches by United States fishermen were derived from the United States Bureau of Commercial Fisheries and later National Oceanographic and Atmospheric Administration (NOAA) published statistics (Bureau of Commercial Fisheries 1940 to 1970; National Oceanic and Atmospheric Administration 1971 to 1991) and other United States Department of Commerce and United States Department of the Interior statistical reports. In addition, catch and catch-per-unit-effort data on penaeid shrimp and menhaden were provided by the National Marine Fisheries Service. (Penaeid shrimp data are from James M. Nance, Galveston Laboratory, National Marine Fisheries Service, Galveston, Texas 77551, and menhaden data are from Douglas S. Vaughan, Beaufort Laboratory, National Marine Fisheries Service, Beaufort, North Carolina 28156.) Trends in landings and, when feasible, stock abundances of estuarine-dependent and non-estuarine-dependent species were examined since 1940 for some species or for more recent time periods for newly-developed fisheries.

The NOAA statistics since 1971 have reported landings within the 0–3 mile zone and offshore. Although catches in the 0–3 mile zone may underestimate the estuarine-dependent yields, we presumed them to be an index of estuarine and estuarine-dependent catches, recognizing that some species produced in estuarine nurseries (for example, a significant fraction of the penaeid shrimp) are caught beyond the 3-mile zone and not properly indexed.

Production and Harvest

Relationships between primary production, fish production, and harvest levels were analyzed for estuarine and marine systems. Data on primary production and fish yields are from Nixon (1982, 1988) and Nixon et al. (1986). We have applied the model derived by Iverson (1990) to predict fish production from primary production, after accounting for the probable availability of "new" nitrogen as a factor influencing sustainable fish production.

The regression relationship between fish harvest and primary production in marine systems developed by Nixon (1988) was used to predict catches in estuaries and other marine ecosystems. Fish production, defined here as the amount of carbon transferred through the food chain to mean trophic level 2.5 (level 0 being primary producers), was predicted in each system from Iverson's (1990) equation. The estimated fishery production and reported catch for ten major estuaries were summarized. In addition, fish production at trophic level 2.5 and predicted sustainable catch were estimated for shelf, upwelling, and oceanic ecosystems.

Global fishery harvests from estuarine, shelf, upwelling, and oceanic systems were predicted using data from Nixon (1988) and applying his regression equation relating fish harvest to primary production. The estimated harvest per unit area in each system was expanded to the total system area by multiplying it by the estimated area encompassed by each system in the world ocean. From Iverson's (1990) equation relating fish production to primary production and Nixon's (1988) regression of fish harvest on primary production, the fraction of fish production that is harvestable was estimated for each system. For this relationship to be valid, the yields of fish from systems reported in Nixon et al. (1986) must be at or near the sustainable level and are presumed to be, on average, near trophic level 2.5. The global fishery production in each ecosystem and, after summing, total world marine fishery production at trophic level 2.5 were estimated. Admittedly, the mean trophic level of harvest is uncertain, but it probably is relatively low in each of the ecosystems, perhaps in the 2.0 and 3.0 range.

For the fish production analysis, mean primary production levels of 57, 162, 225, and 354 g C m^{-2} yr^{-1} were selected to represent oceanic, shelf, upwelling, and estuarine systems, respectively (Whittaker and Likens 1973; Nixon et al. 1986). The mean estuarine primary production estimate is derived from data on ten estuaries (Nixon et al. 1986). Oceanic, shelf, and upwelling mean primary production values are those given by Whittaker and Likens (1973) who had summarized available data. Our global upwelling area, based upon Cushing's (1971) extensive data on seasonal upwelling regimes, is ten times that applied by Ryther (1969) in his estimate of global fisheries production. Our mean primary production estimate in the upwelling systems, taken from the summarized data in Whittaker and Likens (1973), is considerably lower than that assigned by Ryther. The estuary mean primary production value of 810 g C m^{-2} yr^{-1} in Whittaker and Likens (1973) was not selected because recent data (Nixon et al. 1986; Peters and Schaaf 1991) do not support such high values as the annual mean for estuarine systems.

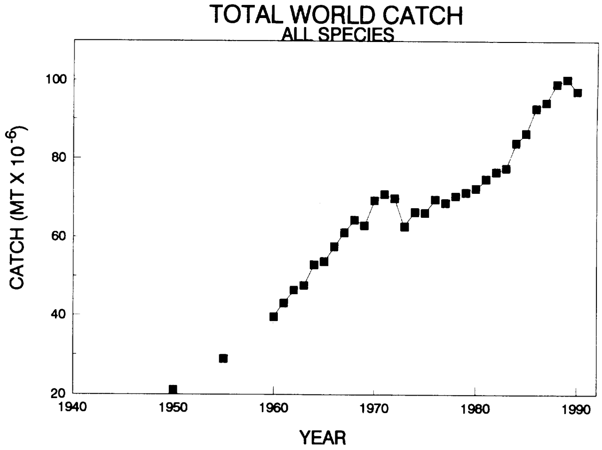

Fig. 1. World landings of invertebrates and vertebrates (from United Nations Food and Agriculture statistics (1955 to 1991)).

Results and Discussion

World Catches

The summed landings of vertebrates and invertebrates have increased more or less continuously since the United Nations Food and Agriculture Organization (FAO) began compiling statistics. The total catch, marine plus fresh water, and including aquaculture, reached 100.3 million metric tons in 1989, but fell to 97.2 million tons in 1990 (Fig. 1). In 1989, the marine catch of 86.5 million tons (86.2%) provided the bulk of landings. Total world catches increased at annual rates of 3.2% per year between 1960 and 1989, and at 2.2% per year since 1970. They increased rapidly, at 3.7% per year, during the 1980s. The marine component of fishery harvests increased at 3.1% per year between 1960 and 1989, 1.9% per year since 1970, and 3.0% per year since 1980. Contributions from aquaculture became increasingly significant after 1975, and by 1990 accounted for approximately 14.5 million tons of products, 10.0 million tons from fresh water and 4.5 million tons from marine systems, respectively. A brief period of declining world landings in the 1970s (Fig. 1) was attributable to the collapse of the Peru anchoveta fishery, which had been the world's single largest fishery (>10 million tons yr^{-1}) prior to declines believed to result from the 1972–1973 El Nino and excessive fishing mortality (Cushing 1982).

Five species, none of which is estuarine-dependent, and each with >3.5 million tons landed, were the most important contributors to the 1989 world catch. Alaska pollock (*Theragra chalcogramma*) (6.3 million tons), Peru anchoveta (*Engraulis ringens*)

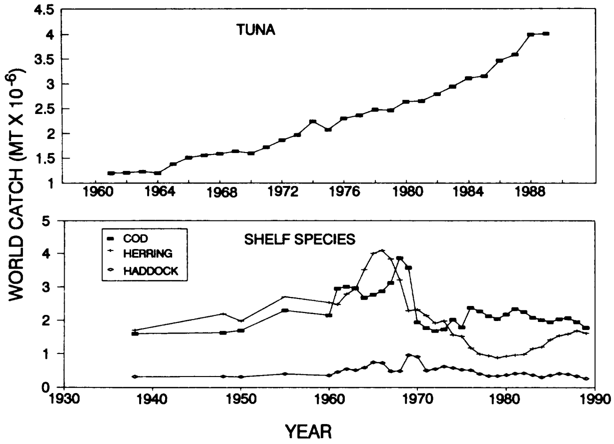

Fig. 2. World landings of tunas, an oceanic species-group (1962–1989), and of cod, haddock, and herring (1938–1989), three traditional, shelf species (from United Nations Food and Agriculture Organization statistics (1955–1991)).

(5.4 million tons), Japanese pilchard (*Sardinops melanosticta*) (5.1 million tons), South American pilchard (*Sardinops sagax*) (4.2 million tons), and Chilean jack mackerel (*Trachurus murphyi*) (3.6 million tons) comprised 24.7% of total world landings and 28.9% of the marine landings in 1989. Perhaps surprisingly, the only estuarine-dependent species included in the top 20 species in world landings during 1989 was the Pacific oyster (*Crassostrea gigas*) (0.6 million tons), which was harvested primarily by aquaculture industries.

Catches of many traditionally-harvested, nonestuarine species and species groups either have increased consistently since 1970 (e.g., tunas), or peaked just prior to 1970 and have declined subsequently (e.g., Atlantic cod, *Gadus morhua*, haddock *Melanogrammus aeglefinus*, and Atlantic herring, *Clupea harengus*) (Fig. 2). The catch of tunas, which reached 4.0 million tons in 1989, has increased at an annual rate of 4.8% since 1970 and continues to increase rapidly, although some species (e.g., Atlantic bluefin, *Thunnus thynnus*) are badly overfished (National Oceanic and Atmospheric Administration 1991). Ryther (1969) believed that little harvesting of oceanic fishes such as tunas was possible, estimating that only 1.0 million tons of annual production occurred at the trophic level he assumed appropriate for top-level oceanic carnivores. Clearly, oceanic fish production at trophic levels available for harvest must be more than an order of magnitude higher than Ryther's estimate to sustain the present catch, as Alverson et al. (1970) had argued. The trends in catches of many traditional continental shelf fisheries (Fig. 2) indicate that these stocks are now fully or overexploited in most regions. In coastal upwelling ecosystems, the FAO records show high landings of

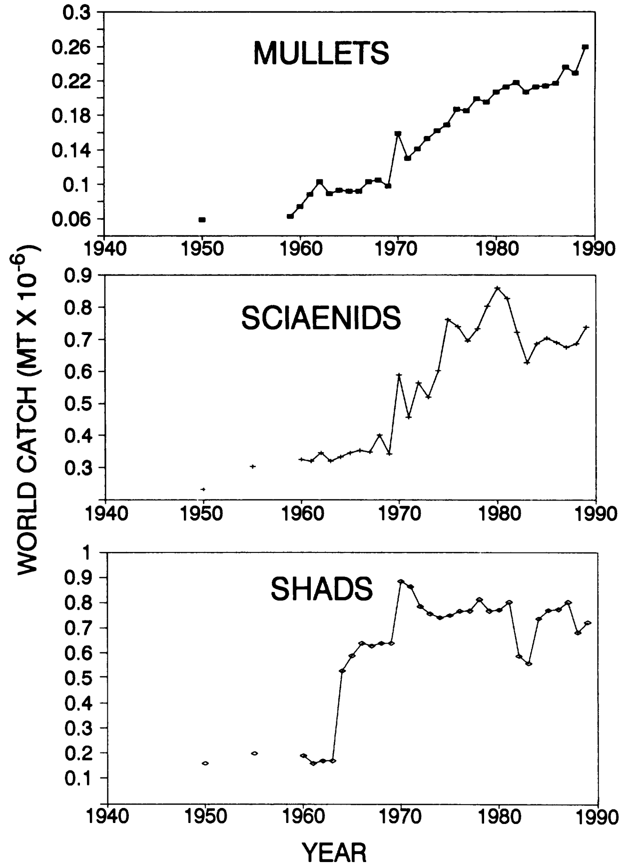

Fig. 3. World landings of mullets, sciaenids, and shads, three groups of estuarine-dependent species, 1950–1989 (from United Nations Food and Agriculture Organization statistics (1955–1991)).

clupeoid fishes and jack mackerels, punctuated by collapses and rebounds that reflect climatic variability and responses of stock levels to fishing effort.

World landings of estuarine-dependent species generally have increased substantially since 1960 (Figs. 3 and 4). On a global basis, there is no indication of collapse of any major species group in the estuarine-dependent category. Shad (alosids) catches increased rapidly during the 1960s, peaked in the 1970s, and possibly declined slightly in the 1980s; sciaenid (drums and croakers) catches increased rapidly in the 1970s, peaked in 1980, and then declined slightly; mullet (mugilids) catches continued to increase throughout the 1960–1989 period (Fig. 3).

Aquaculture production of estuarine-dependent species recently has added significant supplements to wild fishery harvests. World landings of penaeid shrimps, salmons, and oysters all have increased substantially in recent years, and each has a large culture component (Fig. 4). The increase in harvest of wild penaeid stocks averaged 2.2% annually

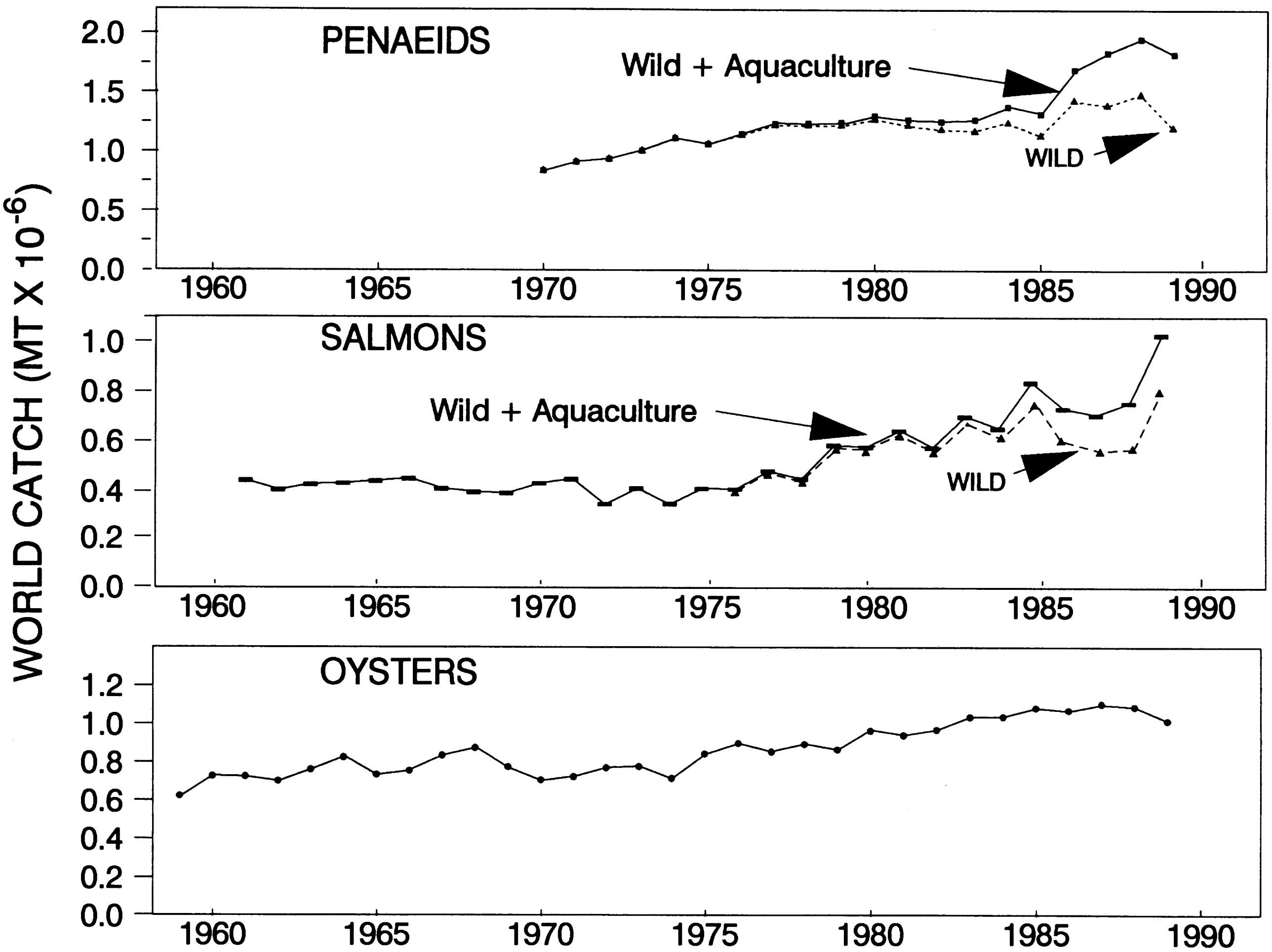

Fig. 4. World landings of penaeid shrimps (1970–1989), salmons (1961–1989), and oysters (1959–1989), three groups of estuarine-dependent species. The component of landings attributable to aquaculture is indicated for the shrimp and salmon (from United Nations Food and Agriculture Organization statistics (1955–1991)).

from 1970 to 1989. At the same time, aquaculture production of penaeid shrimp was increasing rapidly, accounting for approximately 25% of world landings in the late 1980s (United Nations Food and Agriculture Organization 1991), and reportedly reached 690,000 tons in 1991, which accounted for 28% of all shrimp (penaeids plus others) entering the world market (Fishing News International 1992). The world salmon catch has increased surprisingly fast in recent years, despite continued losses of freshwater spawning areas, estuarine degradation, and poorly regulated high-seas fishing. The world catch of salmons exceeded 1.0 million tons in 1989 (Fig. 4). Wild salmon catches nearly doubled since 1970, and aquaculture harvests also grew substantially. An estimated 0.22 million tons of the 1989 landings, mostly Atlantic salmon (*Salmo salar*), came from aquaculture (Anonymous 1991). World oyster harvests have increased slowly in recent decades, and have exceeded 1.0 million tons since 1983. More than 90% of recent oyster landings are from culture industries (United Nations Food and Agriculture Organization 1991).

Coastal aquaculture clearly has become a major contributor to estuarine fish harvests in the past two decades and its role will continue to increase in importance. The production of aquaculture "fish" generally is not totally independent of estuarine productivity, even when supplemental foods are provided. Cultured fish and invertebrates may compete for resources with wild populations, modify the estuarine environment by their waste production, constrain capture fishery operations for wild resources, modify the overall productive capacity of estuaries through nutrient inputs, or contribute to conditions conducive to development of toxic algal blooms that affect both cultured and wild resources. Significant problems and challenges lie ahead to determine the overall potential of coastal aquaculture and its role in estuarine habitat modification.

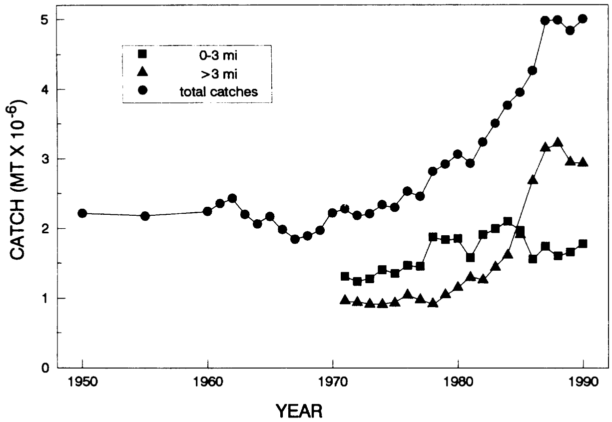

Fig. 5. United States landings of fishery products (1950–1990). Landings in the 0–3 mile zone exclude Pacific cod, Pacific herring, and Alaska pollock, three important species that are not estuarine dependent. Data from United States fisheries statistics, National Oceanic and Atmospheric Administration Current Fisheries Statistics Series (1971–1991).

United States Catches

In 1940, the United States landed 1.8 million tons of fishery products. Landings increased to 2.2 million tons by 1950 and remained stable at the level through 1975, increased to 3.1 million tons in 1980 and to 5.0 million tons in 1990 (Fig. 5). (Total United States landings given here are reported as round (live) weight, including weights of shell for univalve and bivalve molluscs, in accord with United Nations Food and Agriculture Organization practice. In United States landings statistics reported by National Oceanic and Atmospheric Administration, United States Department of Commerce, mollusc landings are reported in weight of meats without shell. Consequently, total landings reported here may not appear to agree with some published United States catch statistics.) The mean annual rate of increase from 1970 to 1990 was 3.8%. Most of the increase during the 1980s was attributed to a single species, Alaska pollock (*Theragra chalcogramma*), whose landings increased from only 1,412 tons in 1980 to 1.44 million tons in 1990. Alaska pollock now is the single largest United States fishery. This species, which is not estuarine-dependent, also was the biggest contributor to world landings in recent years, with 6.26 million tons landed in 1989.

Assuming that catches within the 0–3 mile United States zone primarily index landings of estuarine and estuarine-dependent species, the trend (Fig. 5) indicates a mean increase of 3.5% annually from 1971 to 1984, with a peak at 2.1 million tons in 1984. The subsequent decline to a mean level of 1.7 million tons in recent years suggests that nearshore and estuarine catches may not have been sustainable at the 2.0 million ton level, at least under present management practices and under habitat conditions that now prevail. Catches offshore (>3 mi) of mostly non-estuarine-dependent species were relatively stable during the 1970s at approximately 1.0 million tons, then increased rapidly to more than 3.0 million tons by the late 1980s (Fig. 5), due primarily to the steep rise in United States landings of Alaska pollock. Although most estuarine-dependent species are caught in the 0–3 mile zone, a significant fraction of the 1990 menhaden (15.5%, 138,000 tons) and penaeid shrimp (40.0%, 50,500 tons) catches were caught >3 mi offshore.

Catches of nine major, estuarine-dependent specie sand species-groups comprised nearly 56% of the 1970 and at least 50% of the 1990 United States commercial landings exclusive of Alaska pollock, which was not fished by the United States in 1970

TABLE 1. Catches of some principal estuarine-dependent species in United States fisheries, 1970 and 1990. Data derived from United States Fisheries Statistics, National Oceanic and Atmospheric Administration Current Fisheries Statistics Series.

	1970		1990	
Species	Tons	Percent	Tons	Percent
Menhaden (two species)	824,450	37.1	891,900	30.0
Penaeid shrimp (three species)	114,350	5.2	126,300	4.2
Salmons (five species)	180,300	8.1	333,250	11.2
Oysters[a] three species)	23,000	1.0	13,250	0.4
Blue crab	64,750	2.9	91,750	3.1
Sciaenid fishes (four species)	7,200	0.3	8,500	0.3
Mullet	14,200	0.6	13,000	0.4
Winter flounder	11,000	0.5	6,750	0.2
Summer flounder	2,600	0.1	5,450	0.2
Subtotal	1,241,850		1,490,150	
Total United States catch minus Alaska pollock	2,219,800	55.8	2,977,750	50.0
Total United States catch including Alaska pollock	2,219,800	55.8	4,412,900	33.8

[a] Weight of meats without shell.

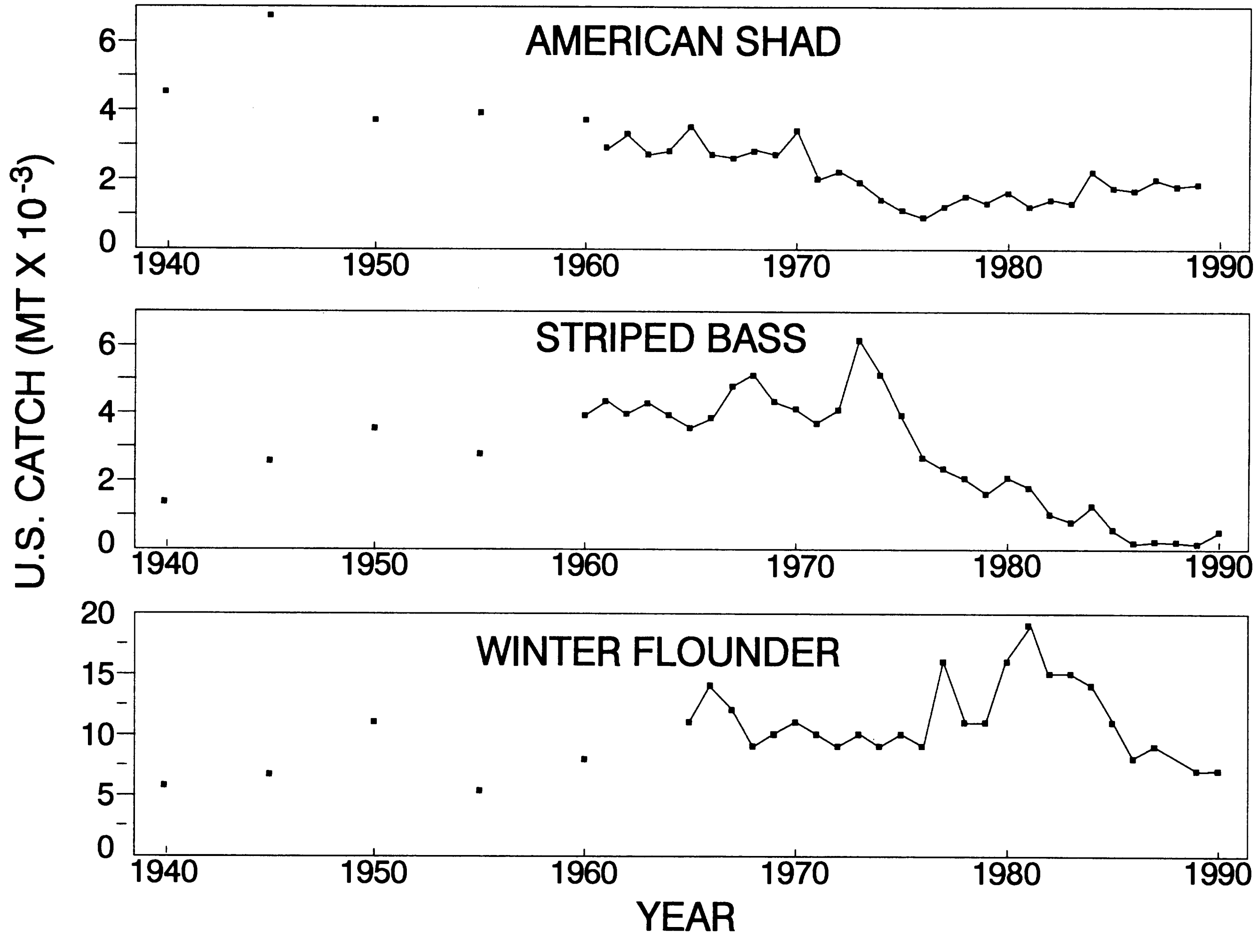

Fig. 6. United States landings of American shad (1940–1989), striped bass (1940–1990), and winter flounder (1940–1990). Data from United States fisheries statistics, National Oceanic and Atmospheric Administration Current Fisheries Statistics Series (1971–1991).

(Table 1). Menhaden (*Brevoortia* spp.), penaeid shrimp (*Penaeus* spp.), salmons (*Oncorhynchus* spp.), and blue crab (*Callinectes sapidus*) predominated in the estuarine-dependent landings, contributing 53.5% and 48.5% in 1970 and 1990, respectively, to the total United States landings exclusive of Alaska pollock. The relative contribution of these estuarine-dependent species (Table 1) declined from 55.8% to 50.0% in the 1970–1990 period, but their total catches did increase (Table 1) from 1.24 to 1.49 million tons in this period. This 20% increase was mostly due to a near doubling in landings of salmons and substantial increases in landings of menhaden, penaeid shrimp, and blue crab. Catches of the other estuarine-dependent species were relatively stable or declined in the 1970–1990 period.

Some estuarine-dependent fisheries in the United States have declined sharply or collapsed on a national or regional scale, in contrast to the relatively stable or increasing catches of estuarine-dependent species on a global scale. Only a few United States estuarine fisheries have remained stable or increased in recent years. United States oyster fisheries, a barometer to many who believe that estuarine fisheries are near collapse, have been in a steady decline during the 20th century. Landings (meats only) plummeted from 40,000 tons in 1940 to 13,000 tons in 1990 and have continuously declined in the 1970–1990 period (Table 1). Most non-salmonid, anadromous fishes and other species that use the estuarine habitat as spawning sites (e.g., winter flounder, *Pleuronectes americanus*) also have experienced precipitous declines in landings (Fig. 6). In a recent resources status report, no "nearshore" or estuarine-dependent United States fisheries were declared underutilized (National Oceanic and Atmospheric Administration 1991). These resources all were categorized as fully or overutilized, or their utilization status was "unknown." The causes of declines generally are attributed to overfishing, habitat alteration or loss, and to the

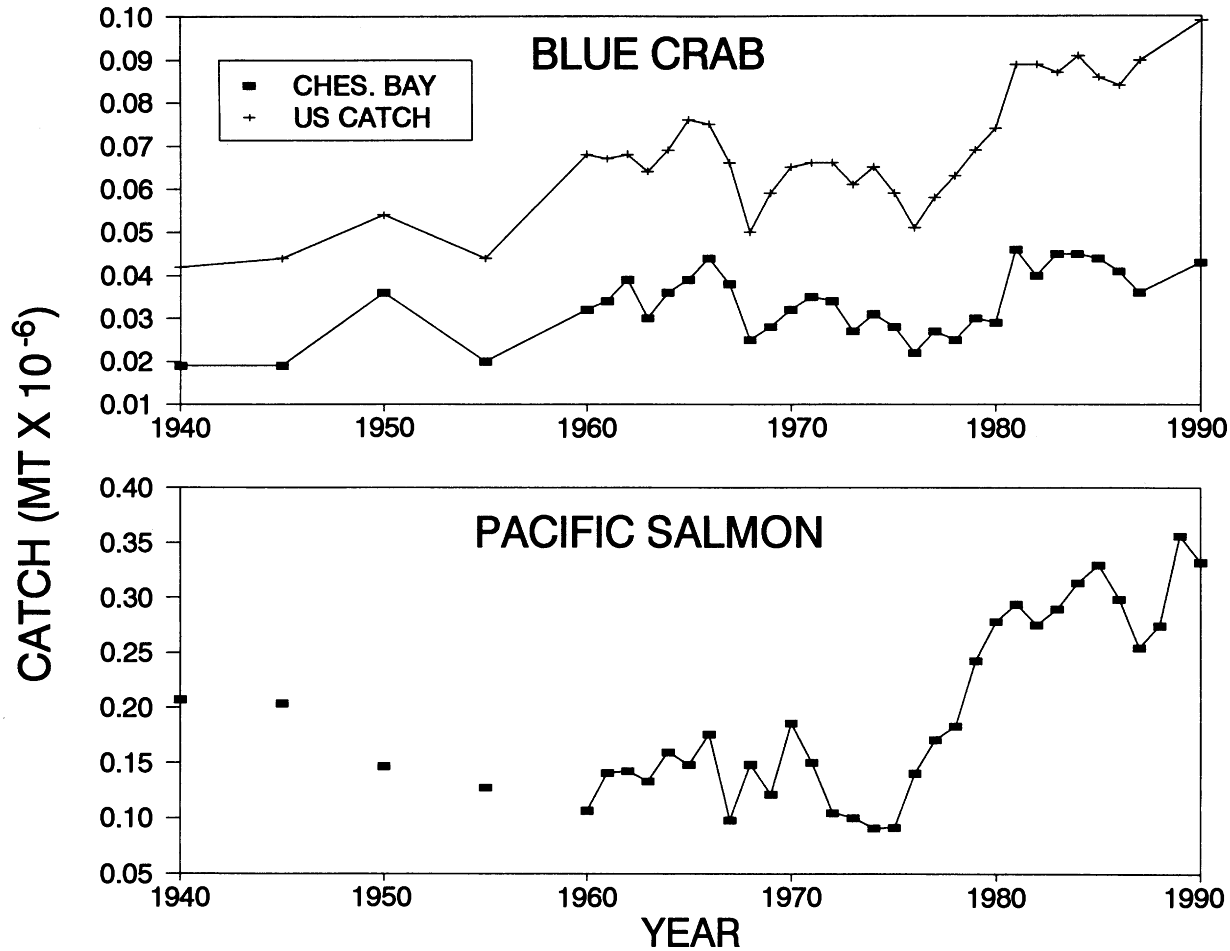

Fig. 7. United States landings of blue crab (United States total and Chesapeake Bay) and Pacific salmons (1940–1990). Data from United States fisheries statistics, National Oceanic and Atmospheric Administration Current Fisheries Statistics Series (1971–1991).

vaguely documented, but probably real, consequences of pollutants and contaminants.

A few estuarine-dependent fisheries have enjoyed increased landings in recent years. The blue crab and Pacific salmons are in this category (Table 1, Fig. 7). Favorable climate and aggressive management and/or restoration efforts in recent years may have favored rebuilding Alaskan stocks of Pacific salmons, which yielded record catches during the 1980s. However, catches of salmon have not increased in California, Oregon, and Washington (National Oceanic and Atmospheric Administration 1991). Blue crab, although now supporting higher landings, probably has done so under significantly increased fishing effort in major areas of exploitation such as Chesapeake Bay (Chesapeake Bay Program 1989).

The Atlantic menhaden (*Brevoortia tyrannus*) and Gulf menhaden (*B. patronus*) fisheries, which together comprise the largest estuarine-dependent fishery resource in the United States (Table 1), have fluctuated extensively during the past 40 years (Fig. 8). After a precipitous decline in the 1960s, annual landings of Atlantic menhaden have been relatively stable since 1970, averaging approximately 300,000 tons. The increase in nominal catch-per-unit-effort (CPUE) may not provide a reliable index of Atlantic menhaden spawning stock biomass in recent years because of increases in the efficiency of purse seine vessels and gears (Vaughan 1990). Spawning biomass of Atlantic menhaden has declined significantly since the 1960s and has remained low throughout the 1980s. In the Gulf menhaden fishery, catches and CPUE have tracked each other closely since 1970 (Fig. 8) (Smith 1991), indicating that its stock biomass has fluctuated at least twofold. Declining catches and CPUE since 1985 suggest that Gulf menhaden population size decreased significantly in the most recent years.

United States landings of estuarine-dependent penaeid shrimps (three species) increased steadily from 1940 until about 1980. Catches (heads on)

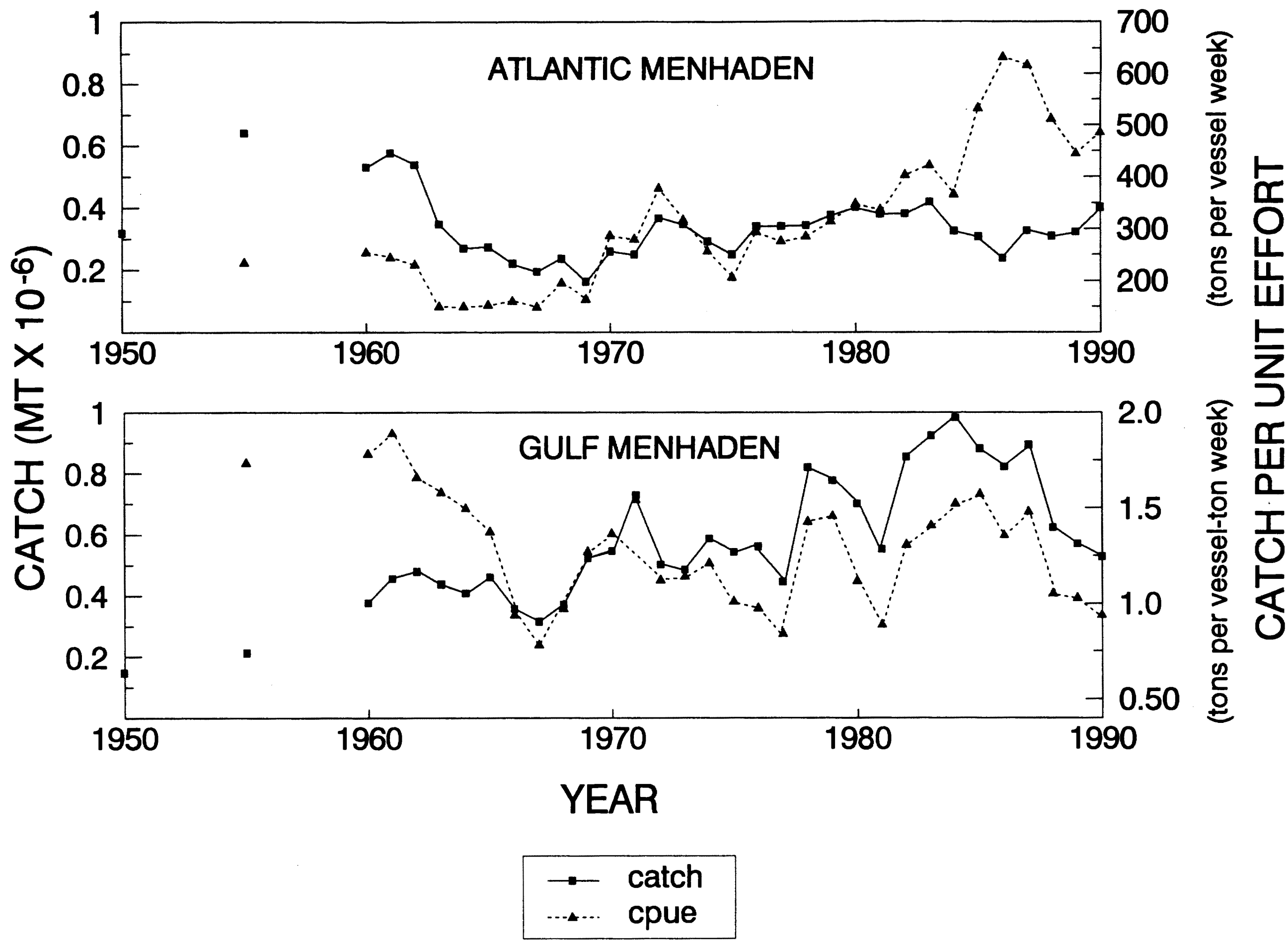

Fig. 8. United States landings and catch-per-unit-effort of Atlantic and Gulf menhaden (1950–1990). Data for Atlantic menhaden from Vaughan (1990) and Smith (1991). Data for Gulf menhaden from Smith (1991).

have fluctuated between 105,000 tons and 140,000 tons in the 1980–1990 period. Most of the catch is made in the Gulf of Mexico, where average landings have increased slowly since 1970 (Fig. 9), except for a brief period in the mid-1970s when an international "petroleum crisis" forced a reduction in fishing effort. There is no apparent trend in the Gulf CPUE during the 1970–1989 period (Fig. 9) that would indicate a significant decline in overall penaeid shrimp biomass. Stock biomass and catches of penaeid shrimp fluctuate primarily in response to recruitment variability, which is controlled by environmental forces (Gulf Regional Fisheries Management Council 1991) that are believed to act principally on young shrimp in the estuarine nurseries. Despite increased landings, the Gulf of Mexico fishery for penaeid shrimps is overcapitalized and a reduction in fishing effort would not significantly reduce the shrimp catch (National Oceanic and Atmospheric Administration 1991), although it would greatly reduce the bycatch and wastage of finfish that is perceived as a major problem in the fishery (Gulf Regional Fisheries Management Council 1991).

Overall, there is need for concern regarding estuarine fishery production and harvest in the United States. This concern is shared worldwide, especially in developed countries where estuarine resources are fully utilized or habitat is being lost and degraded. But, declines in harvest and production of resources are not unique to estuarine stocks. Many traditional fisheries for continental shelf species in the northern hemisphere presently are harvested well below maximum sustainable levels because of poor resource management. For example, United States landings and spawning stock biomasses of yellowtail flounder (*Pleuronectes ferrugineus*) and haddock (*M. aeglefinus*) have declined dramatically to historically low levels (Fig. 10), primarily because of continued overexploitation (National Maine Fisheries Service 1991).

The increase in total United States fishery landings in the past decade is mostly a result of newly-emerging fisheries for Alaska pollock and demersal

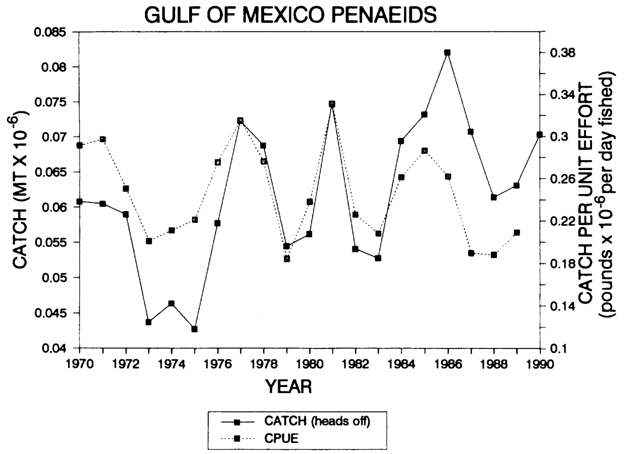

Fig. 9. United States landings (heads off) and catch-per-unit-effort of penaeid shrimp from the Gulf of Mexico (1970–1990) (data provided by James M. Nance, National Marine Fisheries Service, Galveston, Texas). Three species (*Penaeus aztecus*, *P. duorarum*, and *P. setiferus*) were combined fcr ᵗhe analysis.

fishes in the Gulf of Alaska and Bering Sea. Meanwhile, many traditional United States fisheries, both estuarine and shelf, with a few exceptions, have declined significantly during the past two decades. It is fortunate that both estuarine and offshore resources worldwide exhibit a remarkable resiliency in their ability to persist, despite depletion of spawning stock biomasses to levels that in many cases are only a small percentage of the biomasses that existed before fishing began.

Recruitment variability is high and to date unpredictable in estuarine fishery resources, as it is for most organisms in marine environments. Two examples show the extent of variability that exists. Recruitment in white shrimp, a short-lived invertebrate species with an estuarine juvenile stage, varied more than five-fold in the Gulf of Mexico from 1960 to 1989 (Fig. 11) (Gulf Regional Fisheries Management Council 1991). Striped bass is a long-lived, anadromous fish. Variability in Chesa-

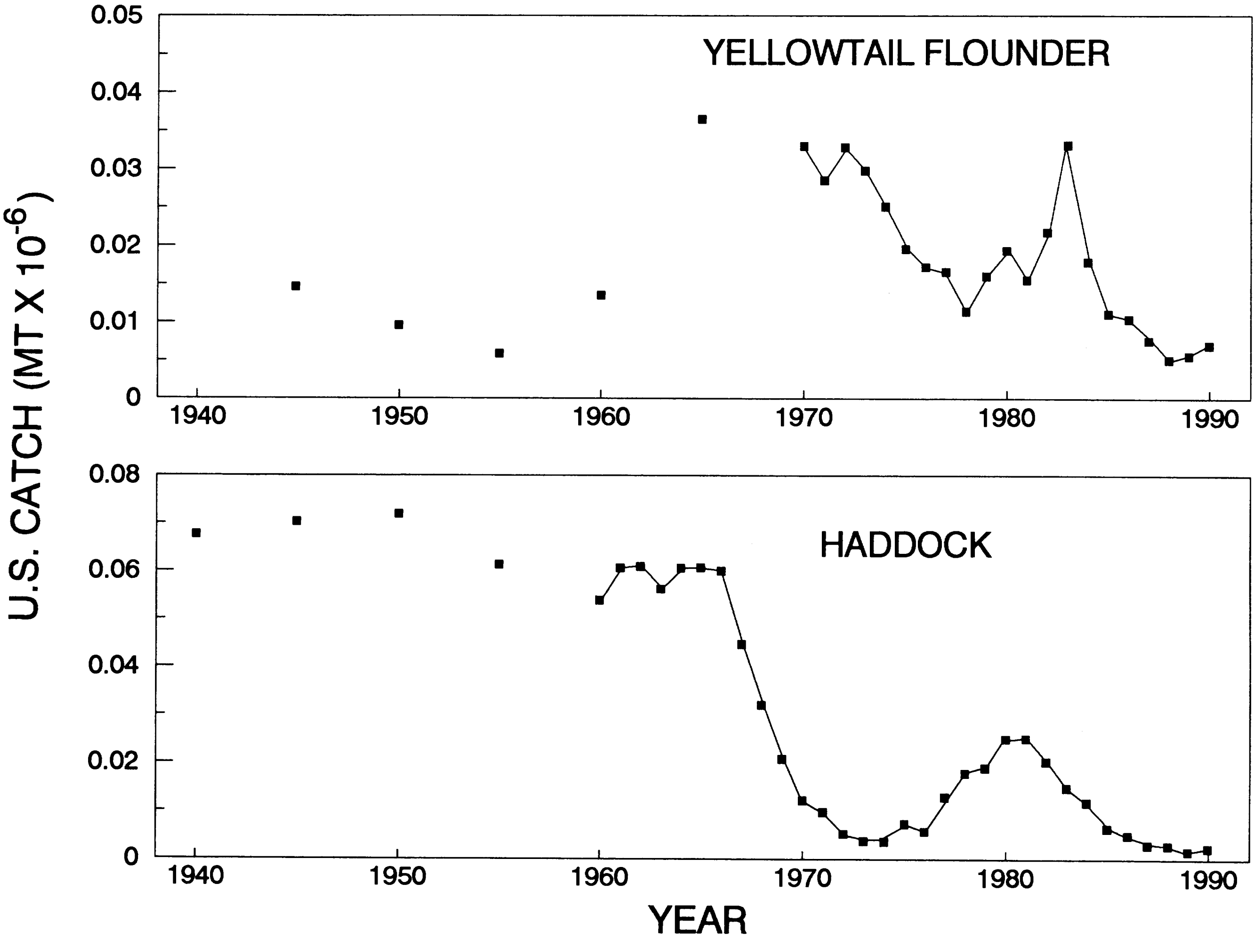

Fig. 10. United States landings of yellowtail flounder (1945–1990) and haddock (1940–1990), two heavily exploited shelf species. Data from United States fisheries statistics, National Oceanic and Atmospheric Administration Current Fisheries Statistics Service (1971–1991).

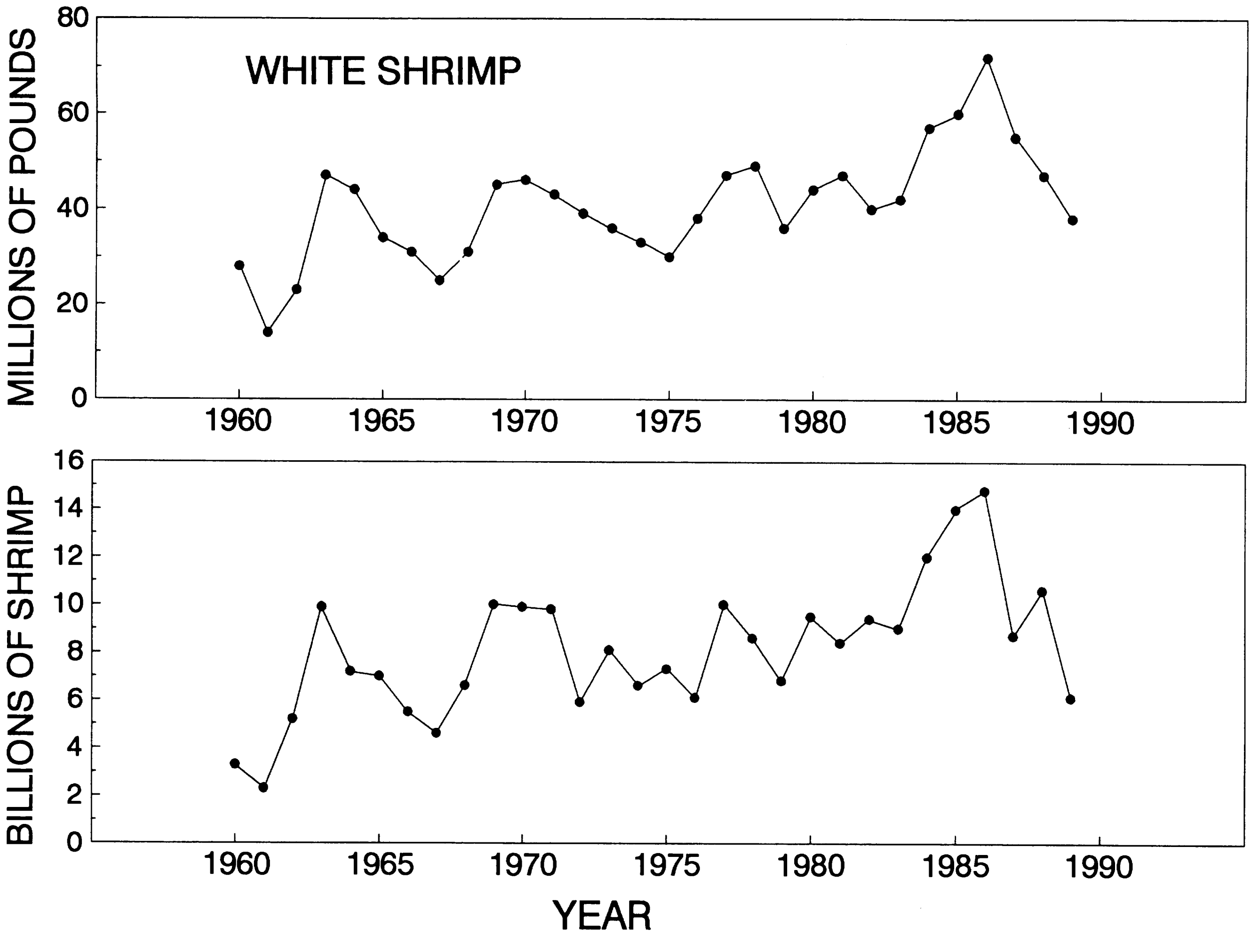

Fig. 11. (top) Landings of white shrimp in the Gulf of Mexico (1960–1989). (bottom) Recruitment variability in Gulf of Mexico white shrimp. Data from Gulf Regional Fisheries Management Council (1991).

peake Bay striped bass recruitments, indexed by juvenile abundance surveys (Fig. 12), varied by at least 30-fold from 1954 to 1990 (Maryland Department of Natural Resources 1991). The fluctuations in recruitment success and inability to predict those fluctuations are persistent problems in fishery science. The magnitude of the problems may be no greater in estuaries than for shelf or oceanic resources, but the consequences to resources eventually may be greater in estuaries where fishing and other anthropogenic influences may converge to impact resources.

Primary Production, Fish Production, and Potential Fish Harvests

It is generally recognized that estuaries are highly productive with respect to fishery resources and that fisheries productivity and yields are related to relatively high primary production, that itself is supported by high nutrient inputs (McHugh 1967; Woodwell et al. 1973; Nixon et al. 1986). Nixon and colleagues have referred to the dependency of fish yields upon primary productivity as the "agricultural model" and have documented a relationship between fish catches and primary produc-

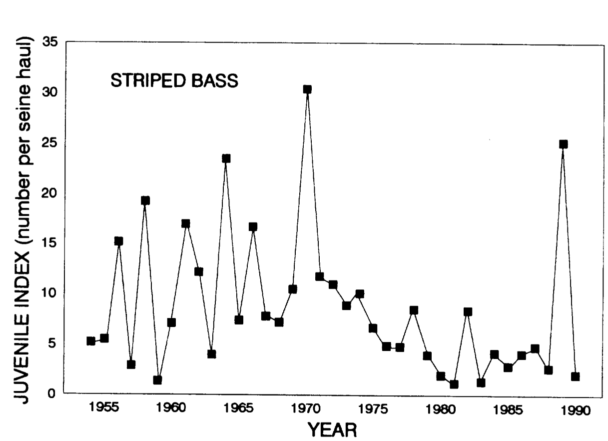

Fig. 12. Recruitment variability in Chesapeake Bay striped bass, indexed by juvenile abundance surveys, 1954–1990. Data from Maryland Department of Natural Resources (1991).

TABLE 2. Primary production, fish catch, and estimated fish production for ten estuarine systems. Primary production and fish harvest are derived from Nixon et al. (1986). Fish production was estimated based upon Iverson's (1990) equation 3, FP = $(-3.08 + 0.083P_0)\cdot E_2^n \cdot c_2$, where P_0 is primary production (g C m^{-2} yr^{-1}), E_2 is nitrogen transfer efficiency (0.28), n is assumed to be trophic level 2.5, and c is the factor to convert g C m^{-2} yr^{-1} to fish biomass (g wet wt m^{-2} yr^{-1}), here taken to equal 36.0. (Note: Iverson (1990) assumed fish carbon to be 12.6% wet wt and consequently c_2 = 28.4; Nixon et al. (1986) assumed fish carbon to be 10% wet wt, which we have accepted, and consequently c_2 = 36.0).

System	A Primary Production (g C m^{-2} yr^{-1})	B Fish Catch (kg ha^{-1} yr^{-1})	C Fish Catch[a] / Primary Production (A ÷ B)	D Fish Production (kg ha^{-1} yr^{-1})	E Primary Production / Fish Production[a] (A ÷ D)	F Fish Catch / Fish Production (B ÷ D)
Narragansett Bay	310	90	0.0029	338	91.7	0.27
Peconic Bay	190	19	0.0010	190	100.0	0.10
Chesapeake Bay	558	200	0.0036	646	86.4	0.31
Pamlico Bay	350	61	0.0017	388	90.2	0.16
Apalachicola Bay	360	270	0.0075	400	90.0	0.68
Barataria Bay	360	300	0.0083	400	90.0	0.75
Delaware Bay	280	7.5	0.0003	301	93.0	0.02
Corpus Christi Bay	180	27	0.0015	177	101.7	0.20
Charlestown Pond	450	100	0.0022	512	87.9	0.20
Great South Bay	500	150	0.0030	574	87.1	0.26
Mean	353.8	122.4	0.0032	392.6	91.8	0.29
Standard Error	39.0	33.1	0.0008	48.4	1.6	0.08

[a] Fish harvest and fish production converted from kg ha^{-1} yr^{-1} to g C m^{-2} yr^{-1}, assuming fish wet biomass to be 10% C.

tion (Nixon 1982; Nixon and Pilson 1983; Nixon et al. 1986; Nixon 1988). Bahr et al. (1982) developed a quantitative relationship between primary production and fish production in the Louisiana coastal zone. Peters and Schaaf (1991) have taken a "top-down" approach to this problem and estimated the "costs" of fish production and reported harvests in coastal waters of the eastern United States, concluding that apparent primary production is insufficient to have supported the observed catches.

Iverson (1990) showed how total primary production is related to new production (i.e., that dependent upon new nitrogen inputs (Dugdale and Goering 1967)), and how sustainable fish production also must be linked to the new nitrogen component in primary production. In Iverson's (1990) model, which we have adopted, potential fish production increases as the fraction of primary production dependent upon new nitrogen increases. Both Nixon (1988) and Iverson (1990) have provided equations that relate potential fish catch in estuarine and marine waters to primary production. In our analyses, we have used Iverson's (1990) equation for fish production and Nixon's (1988) equation for fish catch to explore the potential fishery productivities and yields from estuaries and other marine ecosystems.

The mean primary production (P_o) of ten estuaries, taken from the data of Nixon et al. (1986), is 353.8 g C m^{-2} yr^{-1} (Table 2), which we have accepted as a reasonable, but possibly conservative, mean value of P_o to estimate estuarine fish productions and harvests. This estimate of mean estuarine P_o is lower than some estimates in the reviewed literature (e.g., Koblenz-Mishke 1970 cited in Bunt 1975; Whittaker and Likens 1973, 1975; Woodwell et al. 1973; Peters and Schaaf 1991), which range from approximately 365 g C m^{-2} yr^{-1} to 810 g C m^{-2} yr^{-1}. Fish catches in the ten estuaries, summarized from the Nixon et al. (1986) data, ranged from 7.5 kg ha^{-1} yr^{-1} to 300 kg ha^{-1} yr^{-1} (0.08 to 3.00 g C m^{-2} yr^{-1}), averaging 122.4 kg ha^{-1} yr^{-1} (Table 2). Fish catches in the estuaries always were <1.0% of P_o, averaging 0.32%. Expressed another way, the cost of producing one unit of harvested estuarine "fish" was 312.5 units of net primary production.

Fish production in the ten estuaries (Table 2) was estimated by applying Iverson's (1990) equation at trophic level 2.5 (i.e., midway between primary and secondary carnivore), the presumed average trophic level harvested. Fish production ranged from 177 kg ha^{-1} yr^{-1} to 646 kg ha^{-1} yr^{-1}, mean = 392.6 kg ha^{-1} yr^{-1}. The estimated mean cost of producing a unit of fish carbon was 91.8 units of net primary production carbon. The estimated fraction of fish production that was harvested in the ten estuaries ranged from 2% to 75% (mean = 29%) (Table 2).

If four relatively unproductive Baltic Sea regions had been included in the Table 2 estuaries, based upon Nixon et al. (1986) data, mean P_o for the 14 "estuaries" then would have been only 293.9 g C m^{-2} yr^{-1}. Estimates of mean fishery production and mean harvest also would have declined if the Baltic regions had been included, and the estimated cost of producing a unit of fish carbon would have increased from 91.8 to 96.2 units of P_o.

Using a top-down approach, dependent upon "fish" stomach analysis and estimated mortality rates, Peters and Schaaf (1991) calculated the P_o costs to produce the reported yields of selected United States east coast species, many of which are estuarine-dependent. They estimated a cost of 179 units of P_o to produce a unit of yield (total east coast P_o divided by yield of all included species). The average P_o cost per unit fisheries yield for the ten estuaries in Table 2 (i.e., $1 \div 0.0032 = 312.5$) was considerably higher than the 179 units estimated by Peters and Schaaf (1991) for the estuarine-coastal harvest. If the Baltic subregions were included in our calculation for estuaries, an even higher estimate, 370 units of P_o per unit of harvest, would have been derived, which is approximately equal to an analogous estimate for Georges Bank made by Peters and Schaaf.

Theoretically, fish production and potential catches could be estimated on a global scale for estuaries and other aquatic ecosystems from relationships between primary production, transfer efficiencies, and presumed mean trophic level of harvest (Schaefer 1965). Ryther's (1969) analysis is a classic example of this approach, although there are many other examples (e.g., Schaefer 1965, 1972; Ricker 1969). To our knowledge, none of these analyses has specifically attempted to estimate fishery production and potential harvest for estuaries on a global scale. We have estimated estuarine fish production and potential catches and compared these estimates with estimates for shelf, upwelling, and oceanic ecosystems, arriving ultimately at a global estimate of total fishery production and potential harvest.

The relationships between fishery production, fishery catch, and primary production are illustrated in Fig. 13. The linear relationship between $\log_{10}$ fish catch and $\log_{10}$ primary production (Nixon 1988) is illustrated, and predicted fish catches (kg ha^{-1} yr^{-1}) for oceanic, upwelling, shelf, and estuarine regions are highlighted. Fish production (kg ha^{-1} yr^{-1}) falls off rapidly at low levels of primary production (Fig. 13), reflecting its dependency upon relative amounts of "new nitrogen," a resource that is scarce in oligotrophic regions (Iverson 1990). Ecosystem-specific productions and potential catches are summarized in Table 3. The estimates of mean primary productions and areas were derived from various literature sources, as indicated in footnotes to Table 3.

On a global scale, total primary production (P_o) was estimated to be 24.4×10^9 tons C annually, while total fishery production at trophic level 2.5 was 1.36×10^9 tons wet wt yr^{-1} (Table 3). Globally, fishery production, expressed as carbon, assuming 10% carbon in wet wt, and weighted by the ecosystem areas in Table 3, averages 0.48% of P_o. On average, it requires 208 units of P_o to produce one unit of fish carbon at trophic level 2.5. The *potential* annual fish catch, 307.2×10^6 tons (Table 3), is very much higher than the 1989 world marine harvest of 86.5×10^6 tons. It also is higher than realistic projected harvests that might be attained in the near future. It is unlikely that the large potential catch from the oceanic region, 195.9 million tons (Table 3), can be achieved because of constraints imposed by the dilute distributions of harvestable resources in oceanic areas, limits of harvesting technology, and harvesting costs. On the other hand, the estimated potential catch, summed for the estuarine, shelf, and upwelling regions (Table 3), 111.3×10^6 tons, is very close to world harvest estimates made by United Nations Food and Agriculture Organization (Robinson and Crispoldi 1975; Gulland 1976; United Nations Food and Agriculture Organization 1989b), who suggested that 100 million tons is an approximate long-term sustainable yield of "traditionally-harvested" fishery resources. While the large potential catch from the oceanic regions may never be achieved, it seems certain that catches there could increase substantially, as recent tuna catches indicate (Fig. 2). Under that circumstance, global marine fishery harvest might peak at $>120 \times 10^6$ tons, a $>38\%$ increase over present marine catch levels. Both the observed catch in recent years and potential catch from the oceanic zones are much higher than Ryther's (1969) forecast, a result predicted by Alverson et al. (1970).

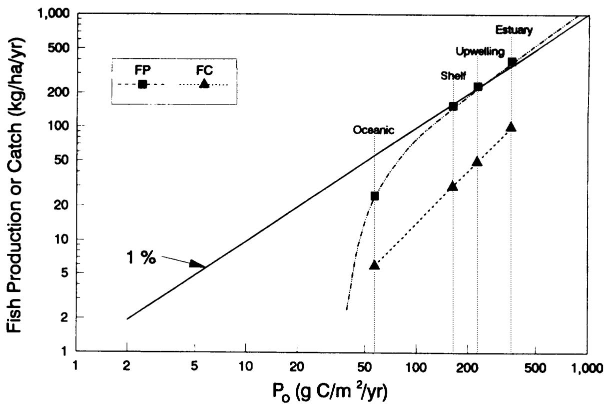

Fig. 13. Predicted fishery production and fishery catches in relation to primary production. Fishery production is predicted from Iverson's (1990) equation: $FP = (0.083\ P_o - 3.08) \cdot E_2{}^n \cdot c_2$, where P_o is primary production (g C m^{-2} yr^{-1}), E_2 is nitrogen transfer efficiency (0.28), n is assumed to be trophic level 2.5, and C is the factor to convert g C m^{-2} yr^{-1} to fish biomass (g wet wt m^{-2} yr^{-1}) here taken to equal 36.0. Fishery catch is predicted from Nixon's (1988) equation: $\log_e FC = 1.55 \log_e P_o - 4.49$, where *FC* is catch in kg ha^{-1} yr^{-1} and P_o is primary production in g C m^{-2} yr^{-1}.

An estimated 2.6% of global marine primary production, 5.2% of fish production, and 5.9% of potential catch may come from estuaries, which

TABLE 3. Estimate of primary production, fish production, and fish harvest potential on a global scale for oceanic, upwelling, shelf, and estuarine ecosystems. Data sources indicated by superscripts and discussed in text. Fish production is at presumed trophic level 2.5.

Region	A Area (10^6 km²)	B Primary Production (g C m^{-2} yr^{-1})	C Global Primary Production (10^9 tons C yr^{-1})	D Fish Production[c] (g m^{-2} yr^{-1})	E Global Fish Production (10^6 tons yr^{-1})	F Potential Fish Catch[d] (g m^{-2} yr^{-1})	G Potential Global Fish Catch[d] 10^6 tons yr^{-1}	H Primary Production / Fish Production[e] (B ÷ D)	I Fish Catch / Fish Production (F ÷ D)
Estuaries	1.8[a]	354[b]	0.64	39.19	70.5	10.02	18.0	90.3	0.26
Shelves	23.0[f,g]	162[f]	3.73	15.48	356.0	2.98	68.5	104.6	0.19
Upwelling	5.0[g]	225[f]	1.12	23.24	116.2	4.97	24.8	96.8	0.21
Oceanic	332.0[f]	57[f]	18.92	2.46	816.7	0.59	195.9	231.7	0.24
	361.8		24.41		1,359.4		307.2		

[a] From Woodwell et al. (1973).
[b] From Nixon et al. (1986) data on ten estuaries (see Table 2).
[c] Fish production as g wet wt m^{-2} yr^{-1}. From Iverson's (1990) equation 3, with $c_2 = 36$ and $n = 2.5$.
[d] Potential fish catches (g wet wt), derived from Nixon's (1988) equation.
[e] Fish production converted g C m^{-2} yr^{-1} by multiplying g wet wt by 0.1 (as in Nixon et al. 1986).
[f] From Whittaker and Likens (1973).
[g] From Cushing (1971). Approximate area derived from coastal upwelling regimes with ≥90 d of upwelling.

TABLE 4. Relative areas and contributions (percent) to production and potential fish harvests of estuaries. shelf, coastal upwelling, and oceanic ecosystems. Fish production is at presumed trophic level 2.5. Percentage values are derived from data in Table 3.

Region	Area	Primary Production	Global Fish Production	Potential Global Fish Catch
Estuaries	0.5	2.6	5.2	5.9
Shelves	6.4	15.3	26.2	22.3
Upwelling	1.4	4.6	8.5	8.1
Oceanic	91.7	77.5	60.1	63.7

occupy only 0.5% of the global marine environment (Table 4). The estimated potential fish catch from estuaries of 18.0 × 10^6 tons yr^{-1} (Table 3) is substantial and may already be fully utilized. The estuarine potential catch is approximately 21% of the recorded world marine catch in 1989.

The relative importance of estuaries to fish production and catches is magnified when their potential is evaluated exclusive of the oceanic region. While occupying only 6.0% of the non-oceanic regions, estuaries are estimated to support 13.0% of fishery production in the estuarine-shelf-coastal upwelling systems, and potentially can contribute 16.2% of the total annual catches from these ecosystems. Potential catches in the global shelf and upwelling regions are 61.6% and 22.2%, respectively, of the 111.3 × 10^6 tons potential of estuary, shelf, and upwelling regions which, while much larger than estuarine potential catches, are smaller in a relative sense than their respective areas (shelf 77.2% and upwelling 16.8%), exclusive of the oceanic zone.

Higher fish catches are possible if the mean trophic level at harvest is reduced. Schaefer (1965) demonstrated the order of magnitude differences in catch levels that are possible if average trophic level at harvest changes. In estuaries, it is uncertain if the option to harvest at lower trophic levels is possible. Overharvests of many resources, environmental degradation and contamination, and collapses of many stocks already have occurred that constrain increasing harvest levels of the primarily benthic, filter-feeding molluscs that live low on the trophic scale and which theoretically could provide relatively large yields. On the positive side, an increased potential of molluscan aquaculture in estuaries seems realistic and might substantially increase estuarine harvests, possibly at the expense of fishery production at higher trophic levels.

An incomplete knowledge of trophic dependencies and transfer efficiencies limits the ability to predict estuarine fishery production and yields. The sources of primary production in estuaries are diverse, and include significant inputs from macrophytes in addition to phytoplankton. Detrital inputs from connected marsh systems also can be important, although their contribution to the cost of fish production still is poorly understood (Peters and Schaaf 1991). Food web analysis (Pimm et al. 1991), network analyses (Baird et al. 1991), "top-down" approaches to evaluate the role of small secondary producers (Stewart et al. 1981), and bioenergetics models (Hewett 1989) all promise to improve our understanding of trophic dependencies and our ability to predict estuarine fish yields in the next decade.

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