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Dependence of Fishery Species on Salt Marshes: The Role of Food and Refuge

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ABSTRACT: Salt marshes are widely believed to serve as nurseries for many fishes and crustaceans of fishery value as a result of the high production of vascular plant detritus and the protection from predation offered by shallow, spatially complex habitats. Comparisons of the yields of species which reside in salt marsh habitats during critical life history stages (such as penaeid shrimp) with the area of such habitats and their greater densities in flooded marshes and associated tidal creeks support the premise that marshes enhance the yield of such species. A range of evidence, including the amount of detrital export from marshes, the poor nutritive value of vascular plant detritus, and natural diets, casts doubt on the notion that production of fishery species is based on the direct consumption of marsh grass detritus or predominantly on food chains based on this detritus. Vascular plants and associated algae may, however, contribute to the production of prey species. The limited observations available support the hypothesis that salt marshes offer significant escape from mortality due to predation, but there have been yet few experimental tests of this hypothesis.

Knowledge of relative importance of the food and refuge functions in support of living resources is of practical value in marsh and fisheries management. Better understanding of these roles is important to the effective evaluation of the effects of coastal habitat modifications on fisheries resources and design of alterations to minimize the losses of these values.

Introduction

It has virtually become an article of faith among American estuarine scientists and environmental managers that salt marshes and other coastal wetlands are important in sustaining fishery species which live in estuaries some or all of their lives. Nixon (1980) reviewed the origins of this viewpoint and found that they were based on assumptions about the nutritive value of organic detritus exported from the marsh and the coincidence of high fishery productivity and salt marsh development. He stated that "it does not necessarily follow . . . that the marshes themselves are the cause of these relationships. Perhaps estuarine-dependent fish simply do well in shallow protected waters, the same environment that usually favors salt marsh development."

We here examine evidence of the rela-

tionship between salt marshes and the production of fishes and invertebrates of economic value by comparisons of yield and standing crop on regional and local scales. Further, we attempt to assess the basis of relationships which exist. To what degree is there a trophic dependence on the production of vascular marsh plants, and to what degree do the salt marshes simply provide a spatially complex habitat offering shelter from predators? We do not imply that this is an either/or question, but, as we will suggest, resolution of the importance of these functional relationships is of practical significance to prudent management of coastal resources.

Fishery Production Comparisons

Nixon (1980) presented evidence which showed that the commercial landings of es-

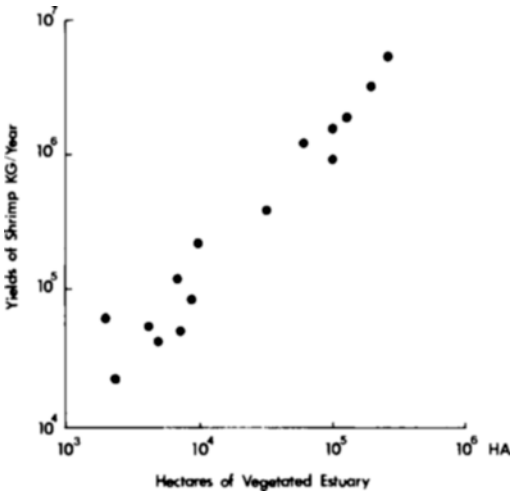


Fig. 1. Relationship between mean annual yield of penaeid shrimp caught inshore (heads-off) and the area of vegetated estuarine habitat in the northern Gulf of Mexico (after Turner 1977).

tuarine-dependent species on a unit area basis are correlated with the ratio marsh area/open water area among the major regions of the U.S. East and Gulf Coasts with one notable exception. The Chesapeake Bay has the highest yield of commercial species (kg/ha) but a rather low marsh to open water ratio. Although such comparisons are made difficult because of the less well bounded nature of the other coastal systems (they do not contain as much open water), more liberal inclusion of nearshore waters in the calculations for the other regions would only exaggerate the discrepancy. Nixon further demonstrated that other coastal ecosystems removed from wetlands have commercial finfish and shellfish yields exceeding those of estuaries which include a large marsh area. However, these are ecosystems which receive large nutrient subsidies from the deep ocean, such as the Peru upwelling region and Georges Bank.

Comparison of multispecies fishery yields with the extent of wetland development is oversimplified and perhaps confusing, even if limited to so-called estuarine-dependent species. The high fishery productivity reported by Nixon for the Chesapeake Bay is substantially due to menhaden (*Brevoortia* spp.), which dominate fishery biomass on both Atlantic and Gulf Coasts. Landings of menhaden are heavily influenced by fishing pressure and effort. In 1966, the year for

which Nixon's comparisons were made, the catch of Atlantic menhaden (*B. tyrannus*, the species caught in Chesapeake Bay) was 2.2×10^8 kg and that of the Gulf menhaden (*B. patronus*) was 3.6×10^8 kg. However, in 1983, the catch of Atlantic menhaden had increased to 3.8×10^8 kg (an increase of 72%), while that of Gulf menhaden increased to 9.2×10^8 kg (an increase of 127%). Landings of Gulf menhaden in Louisiana alone were 7.6×10^8 kg, exceeding the record annual catch of Atlantic menhaden taken in 1956. Thus Nixon's plot of areal yield as a function of the ratio of wetland to open water would be quite different for 1983, with Chesapeake Bay being within the general trend of the relationship (assuming Chesapeake Bay accounted for the same proportion of the Atlantic menhaden catch and constancy in the catch of species other than menhaden).

Turner (1977) compiled data on developed penaeid shrimp fisheries for North, Central and South America and Asia and expressed them in terms of yields per area of vegetated intertidal habitat. Yields were highly negatively correlated with latitude, consequently comparisons can most confidently be made among areas of similar latitude. The average annual yield of shrimp caught inshore in the northern Gulf of Mexico is highly correlated with the area of vegetated wetlands, including grassbeds, within the estuary (Fig. 1), but not with the area, average depth or volume of estuarine water. On the other hand, Doi et al. (1973) found that the yields of *Penaeus japonicus* in the Seto Inland Sea declined in proportion to the loss of intertidal land which was not vegetated.

Additional evidence for the relationship of penaeid shrimp yield and area of wetland habitat comes from the year to year variation in landings in Louisiana. Shrimp landings in Louisiana are positively correlated with salinity during the period of juvenile development (Barrett 1975; Turner 1979). A year with heavy rainfall and high river runoff during the spring and early summer will produce a poor yield, particularly for brown shrimp (*Penaeus aztecus*). In fact, state fisheries biologists are able to make reasonably accurate predictions of fishing success later in the year based on a network

of stations sampled for salinity and an empirical relationship between salinity and temperature during the spring when recruitment and growth are critical. The conventional explanation is that the prevalence of high salinity conditions ($>12\text{‰}$) during dry years increases the area of marsh and shallow waters habitable by juvenile *P. aztecus*, while the suitable habitat is severely reduced during wet years.

Quantitative estimates of the productivity, standing crop, or even density of economically important fishes and invertebrates within salt marshes as compared to open estuarine environments are extremely limited. Several authors have reported a large net export of biomass of fishes and invertebrates from salt marsh creeks (Herke 1971; Yakupzack et al. 1977; Knudsen et al. 1977; Weinstein 1979; Weinstein and Brooks 1983). Mock (1967) reported substantially higher catches of penaeid shrimp in trawl tows adjacent to a salt marsh shore than at 50 and 100 feet from the shore.

Quantification of the utilization of marsh creeks and shallows is hampered by sampling biases and high variability. Weinstein and Brooks (1983) employed drop nets (which provide higher and more realistic estimates than trawls) to measure the densities of nekton in a tidal marsh creek and adjacent seagrass beds in lower Chesapeake Bay. They found that the dominant fish, *Leiostomus xanthurus* (spot), was nearly four times more abundant in the tidal creek than in the seagrass beds. Late in the summer and fall larger spot were found in the grassbeds than in the tidal creek, suggesting that larger individuals were "bled off" from the preferred juvenile habitat in the marsh creek.

Zimmerman and Minello (1984) compared the densities of juvenile *Penaeus* spp. in a Galveston Bay salt marsh to those in an adjacent nonvegetated habitat. *P. aztecus* was nine times more abundant in the marsh when it dominated between March and July. *P. setiferus* was less faithful to the marsh with the average density twice that of the nonvegetated habitat when it dominated between August and January.

In summary, although the evidence is fragmentary, it supports the concept that juveniles of a number of economically im-

portant fishes and invertebrates heavily utilize the shallow habitats associated with the edges of salt marshes and that this is coincident with regional trends of increased yield of those species in areas with extensive salt marshes. However, it should also be pointed out that other co-occurring factors, such as the input of nutrients from terrestrial runoff or the deep ocean, may also influence regional fishery yields (Walsh 1983).

Trophic Dependence

The concept of nourishment of estuarine ecosystems, including their fishery resources, by salt marshes is partially founded on the proposition of "outwelling" of organic detritus from marshes. As Nixon (1980) reviewed, the flux of materials (organic matter and nutrients) into and out of salt marshes is a complex issue and net fluxes vary in magnitude and direction among marshes. Although carbon export from regularly flooded marshes has been estimated to be as high as 50% of the total above-ground primary productivity of the vascular plants, detrital export is near zero in irregularly flooded, microtidal marshes (Borey et al. 1983).

The hypothesis of trophic subsidy is also founded on observations of detritus consumption by estuarine organisms. The studies of Darnell (1958, 1961) on food habits of fishes and larger invertebrates in Lake Pontchartrain emphasized the importance of vascular plant detritus in food chains supporting economically important species. Darnell found the widespread occurrence of such detritus in the guts of fishes and invertebrates and concluded that it was an important food resource for many young fishes, both directly and indirectly by sustaining prey species. Odum and Heald (1975) reported similar results for animals inhabiting a south Florida estuary bordered by mangroves, but emphasized the role of intermediate detritus consumers, such as small crustaceans and insects, in linking detritus and fish production. Naiman and Sibert (1979) also emphasized the importance of organic detritus in support of food chains leading to juvenile salmon production in a British Columbia estuary.

Other arguments for the importance of vascular plant detritus to fishery production

have been based on the apparent insufficiency of primary production of phytoplankton to support the observed secondary production of the fishery. For example, Peters and Schaaf (1981) estimated the food requirements of juvenile Atlantic menhaden in U.S. east coast estuaries by combining data on feeding rates and population size and concluded that the total population consumed more food during its residency in the autumn than is available from phytoplankton or a phytoplankton-based food chain. They suggested that organic detritus, either filtered from the water or ingested from the sediment, is an important alternate source of energy. Such indirect evidence must, however, be weighed with caution because it is not uncommon that phytoplankton production is apparently insufficient to support the observed secondary production of higher consumers, even in ecosystems based virtually entirely on pelagic production. For example, Pomeroy (1979) concluded that in order for enough energy to be carried to terminal consumers of continental shelf ecosystems either the conventional assumption of 10% ecological assimilation efficiency is too low by a factor of 2 to 3, or current measurements of photosynthesis are low by a factor of 5 to 10. Peters and Schaaf's (1981) estimates of food requirements of Atlantic menhaden are based on many compounded assumptions about population densities and feeding rates and they consider only phytoplankton production in waters shallower than 2 m (extrapolated from phytoplankton production measured in only one estuary).

Experimental studies of detritus utilization by macroconsumers have shown that the role of detritus in estuarine food chains is much more complex than Darnell's (1959, 1961) results would suggest. Macroconsumers gain nutrition predominantly from microbes and microfauna associated with the detritus rather than the plant material itself which is nitrogen-deficient as a food source (Tenore et al. 1982; Marinucci 1982). However, there is a lack of experimental evidence that large, metabolically active, and rapidly growing animals such as fishes and decapod crustaceans could use detritus as a primary food source, even if it is microbially enriched.

On the other hand, many small crustaceans, annelids and meiofauna, which are potential prey of fishery species, are known to consume organic detritus (Tenore et al. 1982). Organic detritus in estuarine waters and sediments is composed primarily of small amorphous aggregates, much of which is not of obvious vascular plant origin (Johnson 1974; Van Valkenburg et al. 1978; Ribelin and Collier 1979). This detritus may originate from several sources, including benthic microalgae, phytoplankton, microbes, and aggregates of dissolved organic carbon excreted or leached from plants and animals, as well as salt marsh plants. Ribelin and Collier (1979) found that more than 98% of the detrital material exported from a Gulf Coast salt marsh consisted of amorphous aggregates which were produced primarily by benthic macroflora on the marsh surface rather than by microbial decomposition of the vascular plants.

Assuming that much of the vascular plant detritus exported from a marsh was consumed by detritivorous prey of fishery species and that additional detritus was consumed by such prey residing in the marsh, only a relatively small portion of the energy fixed by the marsh grass would ultimately be available to the higher consumers in the fisheries. Supporting food chains would have a minimum of three steps, i.e., detritus-microbes-detritivore-fish, which would provide to the terminal consumer only 0.1% of the energy in the available detritus assuming 10% ecological assimilation efficiencies between trophic steps. This ultimate yield would be even less if there were additional predatory links (e.g., detritus-microbes-meiofauna-grass shrimp-fish) or if there were more complex microbial mediation, such as chemoautotrophic production (Peterson et al. 1980) (detritus-anaerobic microbes-reduced compounds-chemoautotroph-grazer-fish).

The distribution of stable isotopes of carbon in estuarine organisms places the trophic importance of vascular plant detritus in further question. The stable carbon isotopes, ^{13}C and ^{12}C , are fixed in characteristic and different ratios by primary producers and these ratios presumably change little on assimilation of the organic carbon by consumers. Consequently, the ratio of these iso-

topes in an animal's tissue may be a tracer of the primary producer at the base of its food chain. Haines (1977, 1979; Haines and Montague 1979) reported stable carbon isotope ratios in marsh grasses, phytoplankton, seston and animals in Georgia estuaries and found that suspended detritus and most estuarine animals have ratios closer to that of phytoplankton carbon than *Spartina* carbon. Hackney and Haines (1980) reported similar results for animals near Mississippi salt marshes. Similarly, Thayer et al. (1978) found that animals inhabiting a North Carolina seagrass bed rely more heavily on phytoplankton and microalgae than on seagrass as the ultimate source of carbon; although some species grazed directly on living seagrass.

Fry (1981) found that carbon isotope ratios in the brown shrimp, *Penaeus aztecus*, varied depending on the habitat in which it fed. Shrimp collected from Texas seagrass beds had ratios closer to that of seagrass than those collected from open bays, which possessed ratios closer to that of phytoplankton. Because many shrimp collected on outgoing tides at the estuary entrance bore ratios indicative of grassbed residence, Fry suggested that these habitats may supply more shrimp to the offshore fishery than the deeper estuarine bays.

Interpretation of stable isotope ratios in animals as indicators of trophic dependence is not always simple and straightforward. Organic nitrogen may be a more limiting resource than organic carbon and may be cycled through tissues at different rates. Stable organic carbon isotope ratios are also known to shift between trophic levels (Rau et al. 1983), although at least for pelagic food chains, it is the proportion of ^{13}C which increases. Thus, the isotope ratio would move in the direction of *Spartina* carbon rather than phytoplankton carbon the higher the trophic level.

Another confounding factor in the interpretation of stable carbon isotope ratios as tracers of the relative contribution of vascular marsh plant production is the potential that much of this production is anaerobically decomposed and provides energy through metabolic processes involving reduced sulfur (Peterson et al. 1980). Howarth (1984) estimated that such chemoauto-

trophic production may equal to as much as 10% of the aboveground production by marsh grasses. Reduced forms of sulfur are abundantly produced in marsh and estuarine sediments. Some of this reduced sulfur is chemically oxidized and its energy potential, initially developed through photosynthesis, is lost to the biota. Chemoautotrophic microbes utilize some of the reduced sulfur as an energy source to fix new organic carbon which has isotope ratios specific to the microorganism and not to the plant which produced the original detritus. Thus, if chemoautotrophy is a significant pathway, the energetic contribution of vascular plant production may be underemphasized by the isotope ratio in an animal consumer. The quantitative significance of this pathway is unknown, but the additional trophic steps required and the large sink of chemical oxidation must make it rather inefficient.

In addition to the above rather ambiguous evidence, microscopic, biochemical (Moriarty and Barclay 1981), and immunological (Feller et al. 1979) assessments of food habitats and field experiments (Virnstein 1977; Bell and Coull 1978) suggest that many highly motile estuarine animals, and especially fishes and decapod crustaceans, are primarily carnivorous. This appears true for the economically important portunid crabs (Paul 1981) and penaeid shrimp (Moriarty and Barclay 1981) commonly regarded as detritivores. To be sure, analyses of gut contents often show a high frequency of more or less amorphous detrital material, but it is usually unresolved whether this material is incidentally ingested while foraging. A nutritive value for such material cannot be ruled out. An animal which depends primarily on relatively low quality detrital food would have to ingest large volumes of such material. Consequently, benthic and terrestrial detritivores are characterized by greater gut fullness than is typical for these fishes and crustaceans.

The evidence available to date indicates that economically important fishes and crustaceans depend on food webs which have more bases, pathways and transfer steps than the simple detritivory models previously offered by Darnell (1959, 1961). Although the contributions of planktonic production were probably underestimated

in these models, it is still likely that vascular plants and associated epiphytic and epipellic algae of salt marshes measurably contribute to the secondary production of prey. It is reasonable to assume that the significance of this contribution varies with the availability of marsh versus planktonic detritus. This seems to be borne out in the stable carbon and sulfur isotope ratios of consumers in a New England marsh, which showed gradients indicating planktonic food sources toward the mouths of tidal creeks and *Spartina* sources deep into the marsh (B. J. Peterson, Marine Biological Laboratory, personal communication).

Refuge

Implicit in the concept of salt marsh systems as "nurseries" for economically important fishes and invertebrates is that the shallow waters associated with the marsh provide protection for critical life history stages. In this manner marsh habitats may provide a refuge from predators which would otherwise decimate juvenile populations and lower the potential yield to the fishery. A corollary hypothesis is that the shallow water-wetland interfaces provide habitat and refuge from predators for prey species of the economically important species. This increases the production of prey species and their ultimate availability to the predators.

Anyone who has attempted to maintain a salt water aquarium or bait a hook cannot help but be impressed with the importance of predation in the marine environment. There is, however, woefully little observational or experimental documentation of the refuge function of salt marsh environments. In contrast, there is a more substantial literature on the effects of seagrasses in providing refuge from predators (Orth et al. 1984). Although there are important differences between the two habitats (salt marshes are intertidal and for the most part the animals of concern do not live amidst the grass blades), similar principles regarding the mitigation of predation due to the structural complexity of the habitat may apply.

Heck and Thoman (1981) conducted experiments on the susceptibility of shrimp (*Palaemonetes*) to predation by killifish (*Fundulus*) in containers in which artificial grass leaves were provided as cover. The

density of leaves affected the foraging success of the predators and significant survival of prey was found only at high vegetation densities. Dense *Spartina* culms provided a refuge for amphipods from predation by *Fundulus* in a New England salt marsh (Vince et al. 1976). Predator avoidance may be the principal reason why *Penaeus* aggregates in higher densities in marsh compared to open water as described above from the work of Zimmerman and Minello (1984), but utilization of the marsh for foraging may also be a factor.

In fact, fishes and crustaceans utilizing marsh habitats may be capable of integrating habitat profitability for feeding with risk of predation in selecting a habitat, as has been demonstrated by Werner et al. (1983) for bluegill sunfish (*Lepomis macrochirus*). In their pond experiments, bluegills selected more profitable, unvegetated habitats in the absence of piscivorous largemouth bass (*Micropterus salmoides*). However, in the presence of bass, small bluegills selected the less profitable vegetated habitat to decrease the risk of predation. Growth rates of the small bluegills were consequently reduced in the presence of bass, but growth rates of large bluegills—too large to be preyed on by the bass—actually increased as a result of decreased competition with the small bluegills for the food resources of the unvegetated habitat.

Interesting, but ambiguous, evidence for the refuge value of shallow marsh creek environments is provided by studies of the nekton in marsh impoundments (Herke 1971; Adkins and Bowman 1976). Several studies of closed canals and impoundments for waterfowl management in Louisiana salt marshes have shown that although densities of fishes and shrimp may be lower in enclosed areas, the average size of individuals may be larger. The reduced densities may be a result of limitations the enclosure places on recruitment, but the large size of individuals could either reflect greater average longevity as a result of the relative lack of predators or enhanced growth as a result of reduced competition.

Implications

Although more careful and imaginative research is required to resolve the relative

importance of salt marshes in providing food and refuge, the evidence we have reviewed here provides some support for the refuge hypothesis while indicating that salt marsh detritus is not as directly or substantially important in food chains supporting fishery species than was once thought. However, animals may integrate the food and refuge values of wetland habitats and may find them sites of profitable foraging protection from predators. Moreover, detritus production and nutrient processing by salt marshes may contribute to the enrichment and regulation of estuarine food chains in as yet poorly understood ways. Furthermore, marsh grass production is essential to the perpetuation of this structurally complex habitat, because marshes must continue to accrete sediments and vascular plant detritus (peat) and to grow upward to survive (Hatton et al. 1983).

In addition to the inherent scientific importance of the food and refuge issues, understanding the functional relationships between fishery productivity and coastal wetlands is of great practical importance. For example, is it sufficient to base estimates of the impact of marsh loss or modification on fishery yield by simply extrapolating from yield/area averages (e.g., Turner 1979)? The loss of wetlands in the Mississippi Deltaic Plain of southeastern Louisiana has been measured to be 188,000 ha between 1955 and 1978 (Wicker 1980). Can it be assumed, using an average shrimp yield per unit area of wetland of 33.6 kg/ha for Louisiana and Texas (Turner 1977), that this has resulted in a reduction of 6.2×10^6 kg in potential annual shrimp catch? Is the effect actually less, or might it be even greater? The deterioration of coastal marshes in Louisiana has resulted in saltwater intrusion and an expansion in brown shrimp nursery grounds inland which partially counteract the losses seaward. Is the response of shrimp production to these changes linear, or will it at some point be dramatically geometric?

An understanding of the functional relationships involving trophic support and refuge would be useful for evaluation, design and mitigation of activities affecting wetlands, such as dredging and filling, drainage, and channelization. Although this may seem

a moot issue to those in regions where destruction of salt marshes is virtually prohibited, it is certainly not in Louisiana where the direct removal of over 700 ha of coastal wetlands was permitted in 1981 (Turner 1982), largely for the purpose of oil and gas exploration, extraction and transportation. The area indirectly affected by canal construction may be 10 times that directly removed (Scaife et al. 1983). Economic forces are likely to continue the permitting of such activities. How can they be designed to minimize the reduction in functional values? It is conceivable, of course, but not demonstrated that a modification which results in loss in marsh area, and thus total vascular plant production, may enhance the value of the habitat as a refuge for commercially important organisms or the flushing of detritus to the estuary.

We caution, however, that it is premature to pursue a strategy of creative wetland modification. Given the tremendous losses of wetlands due to the direct and indirect effects of canal construction (Scaife et al. 1983) an immediate management strategy must be to minimize the loss of wetland area. However, when canals are permitted the options for design and mitigation should be evaluated in terms of the functional values we have discussed. For example, bank-side spoil banks appear to interfere with the refuge function of the edge of a natural marsh (Mock 1967) and should be avoided. Spoil banks also interfere with natural marsh hydrology and sediment supply necessary for marsh aggradation to counteract relative sea-level rise. Backfilling and plugging abandoned canals are also frequently considered mitigative options, usually from the viewpoint of encouraging revegetation or restoring natural drainage patterns. These modifications also have implications to refuge function and detrital export which should be considered. Although little is known about these implications, "keep it shallow" would seem to be a good rule of thumb in mitigation engineering.

Finally, we would like to emphasize that the key to fishery management of estuarine-dependent species is coastal habitat protection and enhancement. Following the line of reasoning from wetland loss rates and yield-area relationships as discussed above,

Louisiana may have lost a staggering 6.2×10^6 kg of potential annual shrimp yield (heads off) between 1955 and 1978. However this amount is only about 10 percent of the interannual variation in landings, which is also influenced by a variable and generally increasing fishing effort. The signal of declining production as a result of wetland habitat modification may be hidden by the noise induced by climate and man until it is too late to take corrective actions. Given these relationships, disproportionately little effort in fisheries research and management is devoted to coastal habitat evaluation, protection and enhancement.

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