

The Importance of Habitat to the Early Life History of Estuarine Dependent Fishes

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Abstract.—Habitats for fishes are places where they live and are defined by their physical, biological, and chemical characteristics. During their development, estuarine dependent fishes utilize a wide variety of habitats in the coastal environment as well as within the estuary. Early life-history research has emphasized life-history patterns, abundance, and distribution of fishes in coastal waters and not the habitat they utilize *per se*. Limited data suggest that there are differences in coastal habitat quality that may cause differences in the growth of larvae. Within the estuary, habitats usually have been described by their physical structure, but there is a paucity of data on the actual use of these habitats by larvae and early stage juveniles. We discuss some of the available information for several habitats common to the east and Gulf coasts of the U. S. and conclude that within estuaries the water column and seagrass meadows provide the primary habitats for initial use, but that other habitats are integrally linked through biological, chemical, and physical processes. Because of the coupling between habitats, we recommend that research be addressed more on a basis of landscape, rather than individual habitats.

The habitat of an organism (as defined by Odum 1971) is the place where it lives which frequently changes with developmental stage. Almost 3 decades ago, Hemple (1965) stated that less was known of the transition between larval and juvenile marine fishes than any other life-history stage. Even now we know surprisingly little about the importance of habitat to the larvae of many of our most important species of estuarine fishes. We do know, however, that larvae use a wide variety of habitats during their development, ranging from the continental slope into coastal lagoons, bays, and estuaries up to the freshwater interface.

We also know, without a doubt, that habitat and fishery production are linked, but in most cases these linkages have not been quantified. Many research programs have been, and are being funded to determine the ecological relationships between quality and quantity of habitat and fishery production so that the effects of habitat loss and degradation can be evaluated.

The purpose of this paper is to briefly review the importance of habitat to the larval through early juvenile stages of estuarine dependent fishes, that is, those species utilizing estuarine habitats at some stage of their life cycle.

To determine the effects of habitat loss or degradation on the early life stages, we first need to define the habitat they live in and develop an understanding of ecological factors operating in

those habitats. Once done, we can try to determine how natural or man-induced perturbations might affect the habitat and the organisms that use it. Peters and Cross (1992) have discussed the definitions of habitat and have noted, like Ryder and Karr (1989), that it is defined by its physical, biological, and/or chemical characteristics. They conclude that habitat is most frequently associated with structural components that attract individuals, and that environmental properties such as temperature, toxic substances, oxygen content, and light influence its value and use.

In this paper, we will use Odum's basic definition and describe the place where the specific life stage lives by its physical, biological, and chemical characteristics. As much as possible, we will also identify the critical factors operating in that habitat.

Coastal Habitat

On the southeastern and Gulf coasts of the U. S. there is a wide shelf extending out to the edge of the continental slope. Because coastal or barrier islands usually separate coastal water from estuarine waters, the physical and chemical characteristics of the coastal habitat are more stable than estuarine habitats. Except where affected by large riverine inputs (for example, the Mississippi River) water clarity is usually high. In coastal waters, physical processes that set up "fronts" may play a

significant role concentrating both larvae and their food.

Along the southeastern and Gulf coasts of the U. S., over 90% of the most important commercial and recreational species of fishes spawn in coastal waters. Because of the lack of distinguishing features for estuaries, most early life studies on estuarine dependent fishes have not emphasized the physical habitat as much as environmental conditions.

Hunter (1983) gave a succinct description of how the relationship between larvae and their environment changes with development. During egg and yolk-sac stages, there is an initial increase in the dispersion of eggs and larvae, a high mortality rate, a decrease in overall biomass, and an almost complete dependence on the immediate planktonic habitat in both a physical and biological sense. As larvae develop into the nektonic or free swimming phase they become progressively more independent of the immediate planktonic habitat, are able to search for food, become more aggregated, and the total biomass begins to increase. In this stage, density-dependent factors in the habitat (such as food) begin to become more important.

Water Column

Atlantic menhaden (*Brevoortia tyrannus*), Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and summer (*Paralichthys dentatus*), southern (*Paralichthys lethostigma*), and gulf (*Paralichthys albigutta*) flounders provide good examples of species that utilize the coastal habitat as larvae and early juveniles. These species spawn offshore to the edge of the Gulf Stream. Pelagic eggs are found in the near surface layer and most of the early larvae occur in the upper portion of the water column. We can describe, at least partially, the physical and chemical characteristics of their habitat. In the laboratory, for example, Hettler (1981, 1983) has demonstrated that pelagic eggs of Atlantic menhaden only float in salinities above 26‰ and that the temperature for hatching and survival is between 15 and 25°C.

Early life-history research of fishes from the coastal habitat has concentrated on life-history, abundance and distribution, feeding, growth, and predation. In the 1920s and 1930s, Hildebrand and Cable (1930) described the development and life-history of 14 species of fishes from the vicinity of Beaufort, North Carolina. They concluded that most of the important food fishes taken in the estuary during the summer months migrate to warmer coastal habitats during the fall and winter to spawn.

Subsequent research has confirmed their original hypothesis of offshore fall and winter spawning and estuarine dependence (Dawson 1958; Fore 1970; Powles and Stender 1976; Powles 1981; Judy and Lewis 1983; Shaw et al. 1985).

With the development of sophisticated, depth-discrete samplers, such as the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS, Wiebe et al. 1976), recent studies have examined vertical distribution and behavior of coastal larvae. Sogard et al. (1987) compared the vertical and horizontal distribution of three species of larvae along three transects in the northern Gulf of Mexico, and reported that only gulf menhaden (*Brevoortia patronus*) showed any consistent patterns in vertical distribution, being more concentrated in surface waters. This has also been reported for the Atlantic menhaden (Checkley et al. 1988). Thus, there appears to be some difference in the use of the coastal habitat in the vertical dimension.

For larvae to survive in the coastal habitat there must be ample food. In general, their diets are known to consist of phytoplankters and zooplankters. Early work by June and Carlson (1971) examined the alimentary tracts of late stage Atlantic menhaden larvae and found the contents to be 99% copepods, while Govoni et al. (1983) noted that early stage gulf menhaden larvae had a diverse diet that included phytoplankton and zooplankton. Spot and Atlantic croaker, two related species taken by Govoni et al. (1983) in the Gulf, although feeding on zooplankton, had dissimilar diets that also differed from the diets of gulf menhaden. This suggests reduced competition and partitioning of the habitat with respect to food.

Differences in habitat "quality" may affect growth of larvae over spatial and temporal scales. Studies on age and growth of estuarine dependent larvae have been conducted in both the Atlantic and Gulf of Mexico (Warlen 1982, 1988; Maillet and Checkley 1989). Warlen (1992) found that the average daily growth rate of wild Atlantic menhaden larvae was about 10% greater than for wild gulf menhaden through their first 60 days. He also found different growth rates for gulf menhaden from different coastal areas in the northern Gulf of Mexico and from the same area at different times. Although far from conclusive, this suggests that there may be natural differences in habitat "quality" causing differences in growth to occur in subunits of the overall habitat. Habitat "quality" in a given area may also differ because of seasonal differences in temperature, salinity, food availability, etc.

Plumes and Fronts

Hydrodynamic and physical processes in the coastal habitat act to establish habitat structure. For example, temperature and salinity establish the pycnocline creating a boundary in the vertical dimension. In the horizontal dimension convergence sets up within frontal zones because of wind and pressure gradients. These water column habitat subdivisions, although difficult to study because of their ephemeral nature, may be very important to the survival of larvae.

Govoni and his colleagues have conducted extensive research around the Mississippi River plume in the Gulf of Mexico. They have looked at the spatial distribution, diet composition, condition of larvae, and mechanisms of accumulation of fish larvae in relation to the plume.

Govoni et al. (1989) reported that ichthyoplankton densities about the plume were often greater at the plume front than inside or outside the plume. The difference was, at times, several orders of magnitude. The increased ichthyoplankton concentration along fronts may have biological relevance. There is some evidence that the zooplankton food of the larvae is more abundant in the mixing zone between plume water and shelf water than it is elsewhere (Ortner et al. 1989) and that the phytoplankton biomass is also increased (Dagg et al. 1988).

For example, larval spot were found to have eaten twice as many food organisms in plume water than larvae in shelf waters (Govoni and Chester 1990). However, when Powell et al. (1990) examined the nutritional conditions of spot larvae associated with the Mississippi River plume, they were unable to demonstrate that larvae have a nutritional advantage when associated with the plume fronts. The number of starving larvae was in fact higher in the plume front than either inside or outside the plume.

Estuarine Habitat

Fish larvae that enter estuaries or are spawned within the estuary have a mosaic of habitats to utilize during their subsequent development: seagrass meadows, salt marshes and their tidal creeks, mangroves, unvegetated bottoms, shell reefs, and the water column itself. We will not deal with several estuarine habitat types, such as shell reefs and drift algae, in this paper because of space constraints.

The functional values of habitats in the estuary have been most frequently described for vegetated habitats. The functional roles of seagrasses (Wood et al. 1969) can be equally applied to other estuar-

ine vegetated habitats (Thayer et al. 1978). There are relatively high levels of organic production and high standing crops of plants. Few organisms feed directly on the living plant, and as a consequence, detritus plays a major role. Leaves, stems, and root systems present surfaces for epibiota which are available as food resources and contribute to the overall primary and secondary production of the system. The above-ground structures promote sedimentation of inorganic and organic matter that are important in nutrient cycling and accretion. The physical structure also provides protection from predation.

Unvegetated sediments also provide physical structure (for example, different granulometries, color), chemical composition, and abundant and diverse primary and secondary food resources. Demersal life stages may actively seek refuge from predators using behavioral modifications such as color pattern changes or surface burrowing. They also may seek benthic unvegetated habitats that provide the nutritional resources, but which are in environmental tolerance zones less conducive to predators (that is, combinations of temperature, salinity, and oxygen conducive to growth and feeding, but where predation pressure is lower). The water column itself is also a habitat that provides abundant and varied food resources and environmental conditions that are conducive to growth and survival (Ryder and Karr 1989).

Seagrasses

Of the three vegetated habitats that we discuss, seagrasses have been longest recognized as a critical nursery area and the most frequently studied regarding fishery use. This has occurred because traditional fishery sampling gear could be used routinely with little modification. Being subtidal, seagrass meadows are available to fishes and researchers most of the time, and this habitat type is found in almost all shallow coastal and estuarine waters. Yet, the nursery value of this habitat is generally ascribed to juvenile and subadult fishes with little emphasis placed on the settling larvae or early stage juveniles (Kenworthy et al. 1988; Zieman and Zieman 1989; and references cited therein).

Seagrass meadows consistently have higher abundances and diversities of organisms than unvegetated areas, and densities of food resources (benthic, epibenthic, and planktonic) tend to be higher within seagrass beds. Habitat heterogeneity, plant biomass, and surface area enhance faunal abundances (Stoner 1980). Fishes foraging within

the grassbed canopy are coincidentally protected from larger predators because of grass blade density and surface and because of reduced light penetration (Kenworthy et al. 1988). Additionally, some organisms can orient themselves with the seagrass blades to become camouflaged.

There are few studies dealing with larva settlement and use of seagrass habitats. One might expect, however, that some of the same functions described above for juvenile and subadult fishes would also hold for larvae. Whether larva settlement into habitats is a random or directed process has been the subject of few studies. Bell and Westoby (1986) proposed a model suggesting that larvae settle into the first seagrass bed they encounter and then select micro-sites within the bed; predation pressure is ultimately responsible for abundance and distribution patterns within the bed. Using artificial seagrass habitats with different densities of "leaves," Bell et al. (1987) concluded that abundances of fishes in seagrass beds was not due to larva settlement preferences or post-settlement predation pressure, but rather to the initial availability of larvae to settle indiscriminately into any seagrass shelter. Sogard (1989), using artificial seagrass in New Jersey, has shown that distance from natural eelgrass affects composition of communities. In some instances, fishes and crustaceans apparently traversed expanses of unvegetated habitat to colonize isolated plots of seagrass. This suggests that the "settle-and-stay" (Sogard 1989) hypothesis of Bell and Westoby (1986) may not be the norm. From a limited number of studies such as these, it would appear that we cannot make a definitive statement as to the factors controlling the distribution and abundance of larval fishes within and among seagrass meadows. Predation may play a role, and proximity to other seagrass habitats is important in the composition of the community.

Olney and Boehlert (1988), demonstrated that seagrass beds in the lower Chesapeake Bay were important for fish species brooding eggs (for example, silverstripe halfbeak *Hyporhamphus unifasciatus*) and with demersal adherent eggs (rough silverside *Membras martinica*). On the Pacific coast of the U. S., herring (*Clupea pallasii*) appear to rely on eelgrass blades to attach their eggs. Olney and Boehlert (1988) noted that winter-spring spawners lacked this habitat in Chesapeake Bay, but that seagrass meadows were present and used by larvae of spring-summer spawners: anchovies (*Anchoa* spp.), gobies (*Gobiosoma* spp.), green goby (*Microgobius thalassinus*), sharptail goby

(*Gobionellus oceanicus*), northern pipefish (*Syngnathus fuscus*), weakfish (*Cynoscion regalis*), southern kingfish (*Menticirrhus americanus*), red drum (*Sciaenops ocellatus*), silver perch (*Bairdiella chrysoura*), rough silverside (*Membras martinica*), feather blenny (*Hypsoblennius hentz*), and halfbeaks (*Hyporhamphus* spp.). Sampling in New Jersey vegetated and unvegetated habitats, Sogard (1989) suggested that gobies (for example, naked goby, *G. bosc*) initially settled on sand/mud substrates and subsequently migrated to eelgrass habitats. Subsequent sampling (Sogard and Able 1991), however, did not demonstrate such a pattern.

In contrast, the northern regions of North Carolina exhibit almost year-round coverage of seagrasses (eelgrass and shoalgrass) (Thayer et al. 1984), and larval and early juvenile fishes are present in these beds during much of the year. Early developmental stages of fishes (< 25 mm fork or peduncle length) have been collected from high- and low-energy seagrass habitats near Beaufort, North Carolina between February and August 1991 (NMFS, Beaufort Laboratory, unpublished data). Pinfish (*Lagodon rhomboides*), spot, menhaden, and pigfish (*Orthopristis chrysoptera*), dominated collections during February through April, although numerous other species such as speckled worm eel (*Myrophis punctatus*), gulf flounder, summer flounder, spottail pinfish (*Diplodus holbrooki*), bay anchovy (*A. mitchilli*), striped anchovy (*A. hepsetus*), and mojarra (*Eucinostomus* spp.) were also present. During May through August, total densities were lower, but species composition was higher than during winter, with early stages of gobies, blennies, pipefishes, silver perch, sheepshead (*Archosargus probatocephalus*), searobin (*Prionotus* spp.), mojarras, red drum, and spotted seatrout (*C. nebulosus*) larvae or early stage juveniles becoming common.

Use of this habitat by larvae may be only transitory because these fishes may suffer from heavy predation (Olney and Boehlert 1988). This hypothesis was based on presence of lower numbers of larvae during daylight when planktivores tend to feed than at night and the fact that the early life-history stage probably cannot orient itself to the seagrass blades and thus take advantage of the refuge function of the habitat. If, however, visual detection is important, then the decreased light penetration within the seagrass canopy and the presence of seagrass blades, which can interrupt visual reception and actually camouflage small organisms, should play an equally important role for both early and

later stage fish larvae.

Mangroves

While the functional characteristics described earlier for vegetated habitats may be intuitively correct, the mangrove habitat has received the least attention, particularly as this relates to its nursery function for fishery organisms. As noted by Thayer et al. (1987), Ley (1992), and Thayer and Sheridan (in press), the limited information stems largely from the lack of suitable collection techniques to address the direct contribution of mangroves to fishery organisms. With the exception of some efforts in Australia (for example, Robertson and Duke 1987, 1990) and India (Krishnamurthy and Jeyaseelan 1981), all of the hypotheses and assumptions on nursery value to fishes is derived from sampling of juvenile and subadults, and there have been few experiments carried out to verify the assumptions.

Thayer and Sheridan (in press) have summarized some of the data on species occurring among prop roots of south Florida mangroves. Forage fishes generally predominate: hardhead silverside (*Atherinomorus stipes*), silver jenny (*E. gula*), goldspotted killifish (*Floridichthys carpio*), spotfin mojarrá (*E. argenteus*), code goby (*G. robustum*), rough silverside, striped anchovy, and clown goby (*M. gulosus*), to name a few. Juveniles of commercial and recreational species also are common, but in lower densities: common snook (*Centropomus undecimalis*), gray snapper (*Lutjanus griseus*), spotted seatrout, red drum, striped and white mullets (*Mugil cephalus* and *M. curema*), sheepshead, and great barracuda (*Sphyrna barracuda*). Salinity patterns appear to affect species composition and abundance (Ley 1992). Average juvenile and adult fish density appeared to be low in upstream areas of Ley's (1992) study sites in Florida Bay which were subject to more variable salinities, and high in downstream areas where salinities tended to be more stable. High densities of fishes and invertebrates in mangrove habitats in part may be the result of protection from predators afforded by both the physical structure of the habitat and the frequently occurring high turbidity.

It is quite possible that U. S. mangrove habitats do not serve an important nursery function for larvae of all but resident species. The life-history strategy of many estuarine dependent fishes is one of offshore spawning, immigration of larvae to estuaries, settlement and growth of juveniles, and emigration of sub-adults to offshore or openwater

habitats. Mangrove shorelines frequently are fringed by abundant seagrass habitats. One possible scenario is that larva settlement may occur to a greater extent in the seagrass beds with subsequent movement of early stage juveniles into the mangrove habitat, followed by diel movements between seagrasses and mangroves. In fact, Ley (1992) concluded that paucity of submerged aquatic plants in some areas may result in inadequate intermediate habitat for fishes between planktonic and mangrove life stages.

Thus, we have a poor data base on the direct value to fishery organisms of a habitat that is among the dominant habitats in the tropical and subtropical Americas and which occupies about 200,000 hectares of estuarine and coastal shoreline in the United States. Thayer et al. (in press) recommended research on habitat utilization in several priority areas: development of quantitative sampling methodology for various forest types and the intercalibration of methods for fishery use; comparison of spatial and temporal variation in habitat use by fishes and invertebrates, particularly in relation to critical water levels that permit access; comparing food/feeding ecology and refuge potential in each mangrove habitat; and contrasting these patterns and functions among mangrove, emergent marsh, seagrass, and non-vegetated habitats.

Salt Marshes and Marsh Creeks

Research on the value of *Spartina* and *Juncus* marshes to fishery organisms has dealt primarily with the use of their tidal creeks and with the transfer of energy produced through invertebrates and detritus to fishes (see reviews by Josselyn 1983; Stout 1984; Teal 1986). In the last decade, however, with an increased awareness of the loss of wetlands due to subsidence, sea level rise, and coastal development, there has been a concerted effort to determine the direct use of marsh habitats (that is, the flood marsh surface) by fishes. This includes some experimental studies on functional values of the marsh to growth and survival of fishes.

With the exception of a few studies, there has been little recognition of the potential use by the larval life-history stage. Data suggest that the larvae or juveniles of some species feed extensively on the marsh surface when it is flooded (Weisberg and Lotrich 1982; McIvor et al. 1988; and references cited therein), and that juveniles of many species seek shelter on the marsh surface during high water (Boesch and Turner 1984; McIvor and Odum 1988; Hettler 1989). In light of these findings, one might

expect that a large majority of the fish larvae and early juveniles collected in marsh channels have the ability to move onto the marsh surface on flood tides. Boesch and Turner (1984) noted, however, that there have been few experimental tests of the hypothesis that marsh habitats provide protection from predation for fishes.

There are strong indications that larvae of estuarine transient as well as resident species gain access to marshes and may move actively or passively onto salt marsh surfaces during flood tides, and may be present in sizeable numbers. Talbot and Able (1984) found larval killifishes, silversides, and sticklebacks commonly on three New Jersey salt marshes. Kilby (1955) reported larvae and/or early stage juveniles of these species plus several other species of killifishes, live bearers, and mullets in pools in Florida salt marshes, and Subrahmanyam and Drake (1975), while not sampling marsh surfaces *per se*, demonstrated the presence of 11 to 21-mm spot, mojarra, pinfish, anchovy, and flounder in creeks within tidal *Juncus* marshes. Rountree and Able (1992) also demonstrated numerous species present in New Jersey marsh creeks, but most were classified as young-of-the-year or older; there was little evidence of larvae or very early juveniles being present. Rogers and Herke (1985) showed the presence of < 25-mm individuals of sand seatrout (*Cynoscion arenarius*), spotted seatrout, red drum, gulf menhaden, Atlantic croaker, striped mullet, southern flounder, and sheepshead, to name a few, in interior marshes in Louisiana.

There is little doubt that there are fluxes of material between the marsh surface and adjacent vegetated and unvegetated substrates and the water column in adjacent creeks and the open estuary. In fact, Nixon (1980) has shown that commercial landings of estuarine dependent species are related to the ratio of marsh area to open water area along major areas of the coast with the exception of the Chesapeake Bay. Since 1980, only limited research has been carried out on the direct use of marsh habitats by the early stages of fishes (see previous discussion), and it has emphasized resident and not transient species. It is possible that for the larvae of many species entering an estuary, the water column or seagrass meadows are the major initial habitats of choice (for some demersal species, such as flounders, unvegetated sediments may provide refuge), and that salt marshes or mangroves provide a secondary "choice." Early and later stage juveniles may move readily between habitats, as has been suggested or shown by several investigators

(McIvor and Odum 1988; Hettler 1989; Rountree and Able 1992; Rozaz and Reed 1993). It is obvious that studies are required to address life-history stage use of marsh habitats as well as experimental studies on trophic support and refuge potential, not only of resident species, but also of the transient species that do make use of these habitats.

Unvegetated Bottoms

Unvegetated benthic habitats also present structural complexity for settling larvae within the fluctuating environmental conditions of estuaries. Again, however, much of the information available is on juveniles. Some available scientific data indicate, or at least suggest, that unvegetated benthic sediments provide food and refuge for settling larvae, the latter being a function of sediment granulometry and perhaps color. Marliave (1977) investigated substrate preferences and reported that in many instances larvae preferred substrates that often had characteristics preferred by their adults. This was particularly true for grain size, although frequently there were preferences for color within a grain size; color preference may be related to camouflage. This may be a function of ability to bury, as is the case for marbled sole (*Limanda yokohamae*) and Japanese flounder (*P. olivaceus*), which prefer sand substrates in which they can easily bury (Tanda 1990). Gibson and Robb (1992), however, found that many small (< 30mm) plaice (*Pleuronectes platessa*) failed to bury in fine sediments in the diameter range of 0.062 to 0.125 mm. They suggest that small plaice may be unable to bury completely in any sediment and that this inability may contribute to their vulnerability to predation.

Considerable research on habitat selection by larval and juvenile flatfishes has been conducted (see references in Murchand and Masson 1989; Burke et al. 1991; Gibson and Robb 1992). These studies have examined niche separation in species of flatfishes that may immigrate and settle as larvae in different parts of an estuary. Burke et al. (1991) demonstrated that different habitat preferences for southern and summer flounder were a function of salinity and substrate type. Southern flounder distribution was affected by salinity, being found more frequently between 17 and 24‰, while the summer flounder were unaffected by salinity changes, but were more prevalent on sandy substrates having 99.4 to 99.6% sand. These sediments are more characteristic of downstream sediments than the muddy upper estuary sediments where southern

HABITATS AND POTENTIAL IMPACTS ON FISH

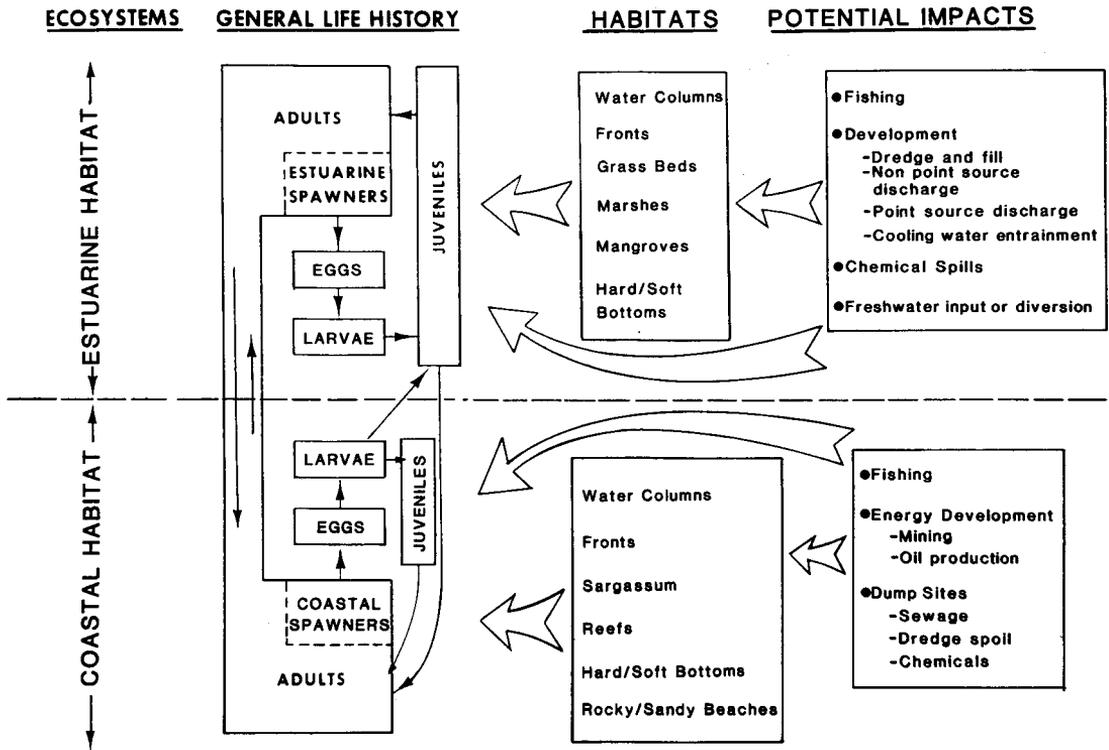


FIGURE 1.—Diagram showing potential environmental modifications to fish habitats and fish life-history stages in coastal and estuarine regions. (See text for discussion).

flounder are prevalent.

Food availability also may play a role in benthic habitat selection by larval flatfishes. Laboratory experiments have shown that summer flounder selected for sand when prey was present in both sand and mud environments, but showed no preference when prey were absent from the substrates (Burke 1991). Edwards and Steele (1968) demonstrated that habitat separation also could occur with plaice, which feed on bivalve siphons, and dabs (*Limanda limanda*), which feed on polychaete tentacles, immediately after settlement.

Summary and Conclusions

Because of the planktonic life style of larvae, changes in the chemical and physical structure of the water column in the coastal zone as well as within estuaries will have the greatest impact (Figure 1). While this is a true statement, it cannot be held inviolate, because many larvae are integrally associated with benthic and vegetated habitats once they have entered the estuary. Additionally,

impacts to these structural habitats will have impacts on future fishery yields because of the associations of early juvenile stages with unvegetated and vegetated environments.

In the open coastal area, disturbances to the integrity of the environmentally favorable water column conditions can have major impacts on larval fishes. For example, alterations to the thermal structure can modify the survival of eggs and utilization of yolk reserves of larvae, making larvae more susceptible to mortality through starvation and/or predation (Figure 1). Particulate and dissolved pollutants, including oil spills, can concentrate along fronts and impact both the food resources of larval fishes and the fishes themselves, both of which may concentrate along fronts (Govoni et al. 1989).

Within estuaries, modifications to temperature, salinity, turbidity, and water chemistry conditions (Figure 1), factors that describe the bounds of the water column and structural habitats, vary over shorter distances or within smaller areas than they

do in the coastal environment, where the modifications generally are more dispersed. Therefore, the already greater environmental stress that occurs in estuaries can be easily exacerbated by slight alterations in water column characteristics. Reduction in oxygen concentration, as might occur with additions of organic substances, or increased concentrations of toxins, as might occur during a chemical spill or through non-point source pollution, can impose additional stress on behavior and growth of larvae and early stage juveniles. Options for juvenile fishes exposed to stressful conditions entail some energetic cost whether it is tolerance of the condition or movement to a less stressful condition (Miller and Dunn 1980); one might consider this to be even more of a monumental effect on larvae than juveniles because larvae have poorer locomotor capabilities and energy reserves. In either case, only limited data exist.

Modifications of freshwater flow such as channelization can impact both water-column and estuarine bottom habitats (Figure 1) and be both beneficial and detrimental to fishery resources. For example, Rogers et al. (1984) found that low-salinity and freshwater areas were primary zones of recruitment for many species and that peak recruitment and use of these areas appeared to coincide with periods of maximum river flow and influence on the estuary, thereby creating a much larger area of optimum habitat. Zimmerman and Minello (personal communication, NMFS Galveston Laboratory), however, found that freshets had a negative impact on fishery organisms in Texas, when fish moved out of the low-salinity area to follow their preferred benthic food resources which were unable to withstand the change in salinity.

Changes in flow patterns that might occur through dredging operations can alter not only the physical structure of the sediment but also its chemical characteristics. Substrates that were once in low-salinity zones and high in silt-clay content or vice versa can be radically altered in terms of both granular structure and color. These modifications can change habitats from optimal to suboptimal for settling larval flatfishes and their prey.

Intuitively, it seems that physical impacts to vegetated and unvegetated estuarine habitats that either remove or modify the physical and chemical structure of the habitat will have a negative impact on most life-history stages that utilize the habitat for feeding, growth, and/or predator avoidance. Nixon (1980) and Boesch and Turner (1984) among oth-

ers, have indicated that there are links between fishery yields and various measures of wetland habitat (acres, ratio of marsh to water, area of marsh edge, etc.), and many have linked the physical loss or contamination of habitat with loss of fishery resources. Evidence of direct impacts of contaminants on fishery organisms as well as on their habitats also have been shown.

We know that impacts of chemical and physical modifications of larval fish habitat have occurred and will continue to occur, in the water column in both coastal and estuarine environments. For many species, impacts to unvegetated benthic habitats and to seagrass meadows also will be detrimental to the survival of larvae because of disruption of food resources and/or refuge areas. Modification to salt marsh and mangrove habitats may have less immediate and direct impacts on larval stages of ocean spawned, estuarine dependent fishes. These estuarine habitats, however, do not exist separately from other habitats within the estuary or the watershed. The components of estuarine systems are coupled through water and chemical exchange as well as through movement of fauna, particularly early and later juvenile stages and even adult life forms (Parrish 1989). Therefore, while marsh and mangrove habitats may not play a major direct nursery role for larval stages, they do so for successive stages.

Management, therefore, must be multidimensional and not directed simply at conservation and enhancement of a single habitat type or a single species. Research needs to address habitat issues on a landscape or hydrologic unit basis with such questions as: what is the sequence of habitats that are used by different life-history stages, both temporally and spatially; what is the optimum mix of habitats to produce optimum growth and survival of species in question; are there obligate and facultative habitats for different species; how does geomorphology (size, shape, edge) influence the use and availability of habitats to different life-history stages; what are the costs of sub-lethal stresses (*sensu* Miller and Dunn 1980).

Acknowledgments

Thanks are due to most of the staff of the NMFS Beaufort Laboratory, Estuarine and Coastal Ecology Division. We thank in particular, Drs. Stanley Warlen, John Govoni, Mr. William Hettler and Ms. Valerie Comparella.

References

- Bell, J. D., and M. Westoby. 1986. Variations in seagrass height and density over a wide spatial scale: effects on fish and decapods. *Journal of Experimental Marine Biology and Ecology* 104:275-295.
- Bell, J. D., M. Westoby, and A. S. Steffe. 1987. Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? *Journal of Experimental Marine Biology and Ecology* 111:133-144.
- Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7:460-468.
- Burke, J. S. 1991. Influence of abiotic factors and feeding on habitat selection of summer and southern flounder during colonization of nursery grounds. Ph.D. Dissertation. Department of Zoology, North Carolina State University, Raleigh.
- Burke, J. S., J. M. Miller, and D. E. Hoss. 1991. Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, USA. *Netherlands Journal of Sea Research* 27:393-405.
- Checkley, D. M., Jr., S. Raman, G. L. Maillet, and K. M. Mason. 1988. Winter storm effects on the spawning and larval drift of a pelagic fish. *Nature* 335:346-348.
- Dagg, M. J., P. B. Ortner, and F. Al-Yamani. 1988. Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico. *Fishery Bulletin, U. S.* 86:319-330.
- Dawson, C. E. 1958. A study of the biology and life-history of the spot, *Leiostomus xanthurus* Lacépède, with special reference to South Carolina. Contributions from the Bears Bluff Laboratory 28.
- Edwards, R., and J. H. Steele. 1968. The ecology of 0-group plaice and common dabs at Loch Ewe. I. Population and food. *Journal of Experimental Marine Biology and Ecology* 2:215-238.
- Fore, P. L. 1970. Eggs and larvae of the gulf menhaden. U. S. Fish and Wildlife Service, Circular 341:11-13.
- Gibson, R. N., and L. Robb. 1992. The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 40:771-778.
- Govoni, J. J., and A. J. Chester. 1990. Diet composition of larval *Leiostomus xanthurus* in and about the Mississippi River plume. *Journal of Plankton Research* 12:819-830.
- Govoni, J. J., D. E. Hoss, and A. J. Chester. 1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*. *Marine Ecology Progress Series* 13:189-199.
- Govoni, J. J., D. E. Hoss, and D. R. Colby. 1989. The spatial distribution of larval fishes about the Mississippi River plume. *Limnology and Oceanography* 34:178-187.
- Hemple, G. 1965. On the importance of larval survival for the population dynamics of marine fish. California Cooperative Fisheries Investigations Report 10:13-23.
- Hettler, W. F. 1981. Spawning and rearing Atlantic menhaden. *Progressive Fish-Culturist* 43:80-84.
- Hettler, W. F. 1983. Transporting adult and larval gulf menhaden and techniques for spawning in the laboratory. *Progressive Fish-Culturist* 45:45-48.
- Hettler, W. F., Jr. 1989. Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. *Marine Ecology Progress Series* 56:111-118.
- Hildebrand, S. F., and L. E. Cable. 1930. Development and life history of fourteen teleostean fishes at Beaufort, North Carolina. *Bulletin of the U. S. Bureau of Fisheries*. 46:383-488.
- Hunter, J. R. 1983. On the determinants of stock abundance. Pages 11-16 in W. S. Wouster, editor. From year to year: interannual variability of the environment and fisheries of the Gulf of Alaska and the Eastern Bering Sea. Washington Sea Grant Publication, Seattle.
- Josselyn, M. 1983. The ecology of San Francisco Bay tidal marshes: a community profile. U. S. Fish and Wildlife Service, Division of Biological Services, Washington, District of Columbia. FWS/OBS-83/23, 102 pp.
- Judy, M. H., and R. M. Lewis. 1983. Distribution of eggs and larvae of Atlantic menhaden, *Brevoortia tyrannus*, along the Atlantic coast of the United States. U. S. National Marine Fisheries Service, Special Scientific Report — Fisheries 774.
- June, F. C., and F. T. Carlson. 1971. Food of young Atlantic menhaden, *Brevoortia tyrannus*, in relation to metamorphosis. *Fishery Bulletin*,

- U. S. 68:493-512.
- Kenworthy, W. J., G. W. Thayer, and M. S. Fonseca. 1988. The utilization of seagrass meadows by fishery organisms. Pages 548-560 in D. D. Hook, W. H. McKee, Jr., H. K. Smith, J. Gregory, V. G. Burrell, Jr., M. R. DeVoe, R. E. Sojka, S. Gilbert, R. Banks, L. H. Stolzy, C. Brooks, T. D. Matthews, and T. H. Shear, editors. The ecology and management of wetlands, vol. 1. Ecology of wetlands. Timber Press, Oregon.
- Kilby, J. D. 1955. The fishes of two Gulf coastal marsh areas in Florida. Tulane Studies in Zoology 2:175-247.
- Krishnamurthy, K., and M. J. P. Jeyaseelan. 1981. The early life history of fishes from Pichavaram mangrove ecosystem of India. Rappports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer 178:416-423.
- Ley, J. A. 1992. Influence of changes in freshwater flow on the use of mangrove prop root habitat by fishes. Ph.D. Dissertation. University of Florida, Tallahassee.
- Maillet, G. L., and D. M. Checkley, Jr. 1989. Effects of starvation on the frequency of formation and width of growth increments in sagittae of laboratory-reared Atlantic menhaden *Brevoortia tyrannus* larvae. Fishery Bulletin, U. S. 88:155-165.
- Marliave, J. B. 1977. Substratum preferences of settling larvae of marine fishes reared in the laboratory. Journal of Experimental Marine Biology and Ecology 27:47-60.
- McIvor, C. C., and W. E. Odum. 1988. Food, predation risk and microhabitat selection in a marsh fish assemblage. Ecology 69:1341-1351.
- McIvor, C. C., L. P. Rozaz, and W. E. Odum. 1988. Use of marsh surface by fishes in tidal freshwater wetlands. Proceedings of the Symposium on Freshwater Wetlands and Wildlife, Savannah River Ecology Laboratory. U. S. Department of Energy, Office of Technical Information, Washington, District of Columbia.
- Miller, J. M., and M. L. Dunn. 1980. Feeding strategies and patterns of movement in juvenile estuarine fishes. Pages 437-448 in V. S. Kennedy, editor. Estuarine perspectives. Academic Press, New York.
- Murchand, J., and G. Masson. 1989. Process of estuarine colonization by 0-group sole (*Solea solea*): hydrological conditions, behavior, and feeding activity in the Vilaine estuary. Rappports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer 191:287-295.
- Nixon, S. W. 1980. Between coastal marshes and coastal waters — A review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. Pages 437-525 in P. Hamilton and K. B. MacDonald, editors. Estuarine and wetland processes. Plenum, New York.
- Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders, Philadelphia.
- Olney, J. E., and G. W. Boehlert. 1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. Marine Ecology Progress Series 45:33-43.
- Ortner, P. B., L. C. Hill, and S. R. Cummings. 1989. Zooplankton community structure and copepod species composition in the northern Gulf of Mexico. Continental Shelf Research 9:387-402.
- Parrish, J. D. 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. Marine Ecology Progress Series 58:143-160.
- Peters, D. S., and F. A. Cross. 1992. What is coastal fish habitat? Pages 17-22 in R.H. Stroud, editor. Stemming the tide of coastal fish habitat loss. Proceedings of the Symposium on Conservation of Coastal Fish Habitat, Baltimore, Maryland. Marine Recreational Fisheries Number 14. National Coalition for Marine Conservation, Inc. Savannah, Georgia.
- Powell, A. B., A. J. Chester, J. J. Govoni, and S. M. Warlen. 1990. Nutritional condition of spot larvae associated with the Mississippi River plume. Transactions of the American Fisheries Society 119:957-965.
- Powles, H. 1981. Distribution and movements of neustonic young of estuarine dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. Rappports et Procès-Verbaux des Réunions, Commission Internationale pour l'Exploration Scientifique de la Mer 178:207-209.
- Powles, H., and B. W. Stender. 1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. South Carolina Marine Resources Center, Technical Report Series 11.
- Robertson, A.I., and N. C. Duke. 1987. Mangroves

- as nursery sites: comparisons of the abundances and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Marine Biology* 96:193-205.
- Robertson, A. I., and N. C. Duke. 1990. Recruitment, growth and residence time of fishes in a tropical Australian mangrove system. *Estuarine Coastal and Shelf Science* 31:723-743.
- Rogers, B. D., and W. H. Herke. 1985. Temporal patterns and size characteristics of migrating juvenile fishes and crustaceans in a Louisiana marsh. Louisiana Agricultural Experiment Station Research Report 5.
- Rogers, S. G., T. E. Targett, and S. B. Van Sant. 1984. Fish-nursery use in Georgia salt-marsh estuaries: the influence of springtime freshwater conditions. *Transactions of the American Fisheries Society* 113:595-606.
- Rountree, R. A., and K. W. Able. 1992. Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance and biomass. *Estuaries* 15:171-185.
- Rozaz, L. P., and D. J. Reed. 1993. Nekton use of marsh-surface habitats in Louisiana deltaic salt marshes undergoing submergence. *Marine Ecology Progress Series* 96:147-157.
- Ryder, R. A., and S. R. Karr. 1989. Environmental priorities: placing habitat in hierarchic perspective. Pages 2-12 in C. D. Levings, L. B. Holt and M. A. Henderson, editors. *Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks*. Canadian Special Publications on Fisheries and Aquatic Science 105.
- Shaw, R. F., W. J. Wiseman, Jr., R. E. Turner, L. J. Rouse, Jr., R. E. Condrey, and F. J. Kelly, Jr. 1985. Transport of larval gulf menhaden *Brevoortia patronus* in continental shelf waters of western Louisiana: a hypothesis. *Transactions of the American Fisheries Society* 114:452-460.
- Sogard, S. M. 1989. Colonization of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. *Journal of Experimental Marine Biology and Ecology* 133:15-37.
- Sogard, S. M., and K. W. Able. 1991. A comparison of eelgrass, sea lettuce, macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine, Coastal and Shelf Science* 38:501-519.
- Sogard, S. M., D. E. Hoss, and J. G. Govoni. 1987. Density and depth distribution of larval gulf menhaden, *Brevoortia patronus*, Atlantic croaker, *Micropogonias undulatus*, and spot, *Leiostomus xanthurus*, in the northern Gulf of Mexico. *Fishery Bulletin, U. S.* 85:601-609.
- Stoner, A. W. 1980. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. *Marine Ecology Progress Series* 3:105-111.
- Stout, J. P. 1984. The ecology of irregularly flooded salt marshes of the northeastern Gulf of Mexico: a community profile. U. S. Fish and Wildlife Service, Biological Report 85 (7.1).
- Subrahmanyam, C. B., and S. H. Drake. 1975. Studies on the animal communities in two north Florida salt marshes. I. Fish communities. *Bulletin of Marine Science* 25:445-465.
- Talbot, C. W., and K. W. Able. 1984. Composition and distribution of larval fishes in New Jersey salt marshes. *Estuaries* 7:434-443.
- Tanda, M. 1990. Studies of burying ability in sand and selection to the grain size for hatchery-reared marbled sole and Japanese flounder. *Nihon Suisan Gakkai-shi* 56:1543-1548.
- Teal, J. M. 1986. The ecology of regularly flooded salt marshes of New England: a community profile. U. S. Fish and Wildlife Service, Biological Report 85 (7.4).
- Thayer, G. W., D. R. Colby, and W. F. Hettler, Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. *Marine Ecology Progress Series* 35:25-38.
- Thayer, G. W., W. J. Kenworthy, and M. S. Fonseca. 1984. The ecology of eelgrass meadows off the Atlantic coast: a community profile. U. S. Fish and Wildlife Service, Biological Services Program FWS/OBS-84/02.
- Thayer, G. W., and P. F. Sheridan. In press. Fish and aquatic invertebrate use of the mangrove prop-root habitat in Florida: a review. *Mangrove ecosystems in tropical America: structure, function and management*. EPOMEX Serie Cientifica (Univ. Mexico).
- Thayer, G. W., H. H. Stuart, W. J. Kenworthy, J. F. Ustach, and A. B. Hall. 1978. Habitat values of salt marshes, mangroves, and seagrasses for aquatic organisms. Pages 235-247 in *Wetland functions and values: the state of our understanding*. American Water Resources Association, Milwaukee, Wisconsin.
- Thayer, G. W., R. R. Twilley, S. C. Snedaker, and P. F. Sheridan. In press. Research information needs on U. S. mangroves: recommendations to the United States National Oceanic and

- Atmospheric Administration's Coastal Ocean Program from an Estuarine Habitat Program-funded Workshop. Mangrove ecosystems in tropical America: structure, function and management. EPOMEX Serie Cientifica (Univ. Mexico).
- Warlen, S. M. 1982. Age and growth of larvae and spawning time of Atlantic croaker in North Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 34:204-214.
- Warlen, S. M. 1988. Age and growth of larval gulf menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico. Fishery Bulletin, U. S. 86:77-90.
- Warlen, S. M. 1992. Age, growth and size distribution of larval Atlantic menhaden, *Brevoortia tyrannus*, off North Carolina. Transactions of the American Fisheries Society.
- Weisberg, S. B., and V. A. Lotrich. 1982. The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog *Fundulus heteroclitus*: an experimental approach. Marine Biology 66:307-310.
- Wiebe, P. H., K. H. Burt, S. H. Boyd, and A. W. Morton. 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. Journal of Marine Research 34:313-326.
- Wood, E. J. F., W. E. Odum, and J. C. Zieman. 1969. Influence of sea grasses on the productivity of coastal lagoons. Pages 495-502 in A. A. Castanares, editor. Coastal lagoons. Universidad Nacional Autonoma de Mexico, Ciudad Universitaria, Mexico City.
- Zieman, J. C., and R. T. Zieman. 1989. The ecology of the seagrass meadows of the west coast of Florida: a community profile. U. S. Fish and Wildlife Service, Biological Report 85 (7.25).