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A Conceptual View of Environment-Habitat-Production Linkages in Tidal River Estuaries

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ABSTRACT: Conservation of aquatic resources requires management of both fishing effort and the mosaic of habitats used by nekton that sustain fisheries production. Within this context, "environment" is viewed as the sum of the abiotic and biotic surroundings, including habitat and other organisms, whereas, "habitat" is viewed as the localized structured component that acts as a template of organization and attractor for nekton. Although there is much debate, it is generally believed that nekton survival depends upon approaching their physiological optima first and then behaviorally searching out the appropriate life-stage-dependent habitat. Deviation from the optimal environment increases mortality and/or decreases production. This conceptual view possesses both dynamic (physical-chemical) and stationary (structural) components. Young estuarine-dependent nekton respond hierarchically to environmental conditions which will "deliver" them into the optimal nursery zones within the landscape leading to higher survival, growth, and production. Variability in climatic conditions coupled with large-scale El Niño-Southern Oscillation (ENSO)/LaNiña events influence recruitment and can shift the position of the dynamic component such that it either does not overlap the stationary component or does so infrequently and only to a small degree. Under these conditions, habitat is considered a limiting factor when these two components are spatially/temporally uncoupled or when access to the structural component is lost due to development or other anthropogenic impacts. For example, habitat alteration due to bulkheading/filling eliminates or reduces access to intertidal salt marshes, which are vital to estuarine ecosystem processes. Additionally, these anthropogenic activities also lead to habitat fragmentation, a change in the spatial arrangement of important habitats along the estuarine axis, and potentially to shifts in the source/sink balance of the estuary. These changes can alter ecosystem health, dynamics, and ultimately productivity. Understanding linkages between these components of the environment is important to aquatic management. The focus of this article is to present a conceptual model that links the environment-habitat mosaic with production, and to illustrate the impact of habitat loss on estuarine productivity. This approach is valuable for 1) predicting the outcome of perturbations, 2) development of a better understanding of the linkages between components of the environment, and 3) providing a basis for future research using a more holistic approach.

KEY WORDS: environment, habitat, linkages, nekton.

I. INTRODUCTION

Factors influencing recruitment are one of the most studied but perhaps least understood components of fishery science, although a better understanding of these important relationships might perhaps help to reduce the trend of fisheries stock collapses worldwide (Houde and Rutherford, 1993; Myers et al., 1996, 1997). Fisheries recruitment and spawning stock size are usually not strongly correlated, while postlarval, juvenile, and subadult abundance and recruitment rates are often positively correlated (Crecco and Savoy, 1984; Rothschild, 1986; Sogard, 1992); however, see Myers and Barrowman (1996). Views of the factors influencing recruitment success have over the last two decades shifted from the more traditional "spawning stock size recruitment" paradigm to one of a search for mechanisms underlying recruitment success whether driven by variable environmental conditions (e.g., Nelson et al., 1977; Bailey, 1981; Bartsch et al., 1989; Cowen et al., 1993; Jenkins et al., 1997), biotic interactions (reviewed in Levin et al., 1997), or a synthetic approach recognizing both components are scale-dependent and thus may influence recruitment success at various life-stage time periods (e.g., Rothschild et al., 1989; Rose and Leggett, 1989; Fogarty et al., 1991; Caley et al., 1996; Hinckley et al., 1996; Jenkins et al., 1998). It is clear that reduced stock abundance due to fishing, hydrography, trophic relationships, and mortality can all affect recruitment, distributions, and trends therein, in space and time. Jenkins et al. (1998) suggested five major components that cause affect of recruitment variability: input of propagules into a given water body, transport of those propagules, planktonic mortality, settlement, and post-settlement growth/survival. Reviews of a number of recruitment hypotheses can be found in Houde (1987), Anderson (1988), Miller et al. (1988), Cushing (1990), Heath (1992), Leggett and DeBlois (1994), and Borja et al. (1996).

In this review, focus will only be on factors considered important to successful recruitment of estuarine-dependent fishes and mobile invertebrates (collectively called nekton) from offshore spawning sites to estuarine settlement habitat, and will highlight the relative importance of habitat to successful recruitment. This review focuses on the nekton that use habitat (as defined later) and does not necessarily relate to more pelagic species of nekton like menhaden silversides or anchovy. This approach incorporates concepts of the Fry paradigm (Fry, 1947; Ryder and Kerr, 1989) and the Hutchinsonian niche (Hutchinson, 1958). Recently, Neill et al. (1994) have conceptualized the importance of the Fry paradigm to better understand recruitment success in flatfishes. I will provide only enough details about mechanisms of recruitment to coastal landscapes necessary to make and support my viewpoint. Using available peer-review data and information on the connections between habitat and abiotic and biotic conditions, I will develop a conceptual model of the connections between environment-habitat-production in tidal river estuaries. The approach outlined is valuable for 1) a better understanding of the linkages between components of the environment, 2) predicting the outcome of natural and anthropogenic perturbations, and 3) providing a basis for future research using a more holistic approach.

II. DEFINITIONS

The functional value of estuaries as nurseries for juvenile nekton has been attributed to 1) physiologically suitable physiochemical conditions, 2) abundant prey resources and appropriate space, and 3) interacting organisms other than those functioning as resources such as predators, competitors, and mutualists (Joseph, 1973; Safriel and Ben-Eliahu, 1991; Chesney and Baltz, 2000; Minello et al., 2003). These attributes illustrate the linkages among abiotic and biotic variables of the estuary that drive estuarine productivity. There is a need, however, for a consistent usage of terms like habitat and environment within a landscape paradigm (*sensu* Chesney and Baltz, 2000). Safriel and Ben-Eliahu (1991) defined habitat as "the environment of a community confined to a portion of the landscape." McCoy and Bell (1991) defined "habitat structure" from a landscape view as the "... arrangement of objects or features in the environment." Baltz (1990) defines habitat as "... the kind or range of environments in which a species/population/life history stage can live." Ryder and Kerr (1989) have defined environment as the "... total physical, chemical, and biological surroundings of an organism, including habitat and other organisms." They view environment and habitat hierarchically as "... the pervasiveness of relatively structureless environment which provides background ambience, against the localized and highly structured habitat which acts as a center of organization and attractor for fish (and nekton) communities." Their view is less ambiguous than the others and I feel this approach is appropriate because it recognizes the synergy between abiotic and biotic components of the environment, and can be interpreted in a landscape perspective. Because estuaries are but one component of the coastal ecosystem landscape, organisms that use estuaries during a portion of their life history must, by definition, encounter a number of "environments" and "habitats" (*sensu* Ryder and Kerr, 1989), which can be selected from and ultimately act as a template on which population and community dynamics occur (Southwood, 1977, 1988; Gibson, 1994).

III. ESSENTIAL FISH HABITAT LEGISLATION

The essential fish habitat (EFH) provisions of the federal Magnuson–Stevens Fishery Conservation and Management Act (MSFCMA) of 1996 mandate that spatial and temporal relationships between fishery species and habitats be included in fishery management plans (Rosenberg et al., 2000). Essential fish habitats are those that provide water and substrate necessary to fishes for spawning, feeding, or growth. In fact, Langton et al. (1996) defined essential habitats as "geographically or physically distinct areas that one or more species finds indispensible for its survival at some phase of its life history." Typically, EFH is associated with structured habitats like submerged aquatic vegetation (SAV), seagrass, mangrove, or salt marshes (Kilgore et al., 1989; Deegan et al., 1997; Jackson et al., 2001a; Jones et al., 2002), but this is not always the case (e.g., Meng and Powell, 1999), as many pelagic nekton species like menhaden, silversides, and anchovies comprise a significant biomass component of estuaries and appear to not require habitat structure. It is estimated that 60–75% of the commercially and recreationally important nekton species of the

Gulf of Mexico (GOM) and the southeastern United States depend on wetlands during a portion of their life cycle (Chambers, 1992). The use of structural habitat by estuarine organisms is, however, variable and depends upon species and life history stage (e.g., Baltz et al., 1993; Edgar, 1999a, 1999b; Hendon et al., 2000; Rozas and Zimmerman, 2000; Pederson and Peterson, 2002). To address the species/stage-dependent linkages between habitat and fishery stocks, the National Marine Fisheries Service has identified four levels of analysis: Level 1 = presence/absence; Level 2 = habitat-related densities; Level 3 = habitat-related growth, reproduction, survival rates; and Level 4 = habitat-related production rates. These sequential levels are used to progressively assess EFH for managed fisheries species (Minello, 1999). The maintenance of EFH, which requires consideration of quality and quantity of that habitat, is vital to the health of an ecosystem, but these ecosystems are subject to climatological effects and human influences. Long-term trends in climatological variation and habitat modification within and among years may strongly influence recruitment (Chesney and Baltz, 2000). In fact, a recent review of the influence of fishing trawls and dredges on habitat complexity as it relates to fisheries indicated that there are only two management tools that can abate/ameliorate habitat loss: 1) habitat protection and 2) habitat restoration (Turner et al., 1999).

Unfortunately, the window of opportunity is quickly narrowing for obtaining quantitative baseline data useful for EFH delineation, because estuarine habitats are being altered at a rapid rate (Chambers, 1992; Hoss and Thayer, 1993; Suchanek, 1994; Thayer et al., 1996; Turner et al., 1999; Peterson et al., 2000b). The passage of MSFCMA legislatively acknowledges the direct link between fisheries production and the integrity of aquatic habitats, but it is urgent to describe and identify EFH within the context of the landscape before baseline relationships change (Rubec et al., 1998). Regardless of the species or life stage examined, thinking of these habitats relative to the source/sink paradigm (Pulliam and Danielson, 1991; Dunning et al., 1992; Crowder et al., 2000) suggests some will be essential and critical (sources); others will be poor (sinks) with a number of habitats forming a gradient of quality in-between the two extremes. Development of a conceptual framework will allow an examination of the cost/benefit trade-offs facing nekton if they are excluded from essential or critical habitat or may only have suboptimal habitat available. Finally, Dunning et al. (1992) indicated that population sizes decrease when the landscape increases in sink habitat relative to source habitat. This suggests that as the source/sink balance changes with habitat loss, habitat quality and ecosystem health decrease. This source/sink balance shift due to freshwater habitat alteration in the Thompson River, British Columbia, has been speculated by Bradford and Irvine (2000) to be deleterious to salmon populations.

Perhaps a better approach is to consider EFH as "requirements" on a sliding scale that considers the fact that the relative spatial position of "hydrologic" and "habitat" environmental components varies temporally and with continuing estuarine modification. This may lead to consensus on distinction between which habitats are "essential" and which are "critical." Essential is defined as "fundamental or absolutely necessary; indispensable," whereas critical is defined as "important, with regard to consequences" (Anonymous et al., 1981). The latter definition suggests a gradient in consequences of habitat use which Demers et al. (2000) terms "rate-determining" habitat. Clearly, not all critical habitats are essential, and one can interpret these habitats as hierarchical in nature with essential habitats being the optimal in all respects, whereas critical habitats provide quality but less-than-optimal conditions. Additionally, one must recognize that there is an ontogeny to habitat use patterns in many nekton, and that part of any definition of nursery habitat should include the habitat that these organisms migrate into once they leave the nursery (Beck et al., 2001; Minello et al., 2003) because that habitat is required to complete the cycle of recruitment to the fishery. Obviously, the importance of any habitat will vary with species and life stage, and it is clear that management of EFH requires detailed examination of several economically important and/or ecologically critical species that can serve as indicators of overall quality of the habitat in question.

IV. IMPORTANCE OF SCALE IN DETERMINING FACTORS INFLUENCING RECRUITMENT SUCCESS

If one examines recruitment processes from a hierarchically based landscape perspective, it appears that oceanographic features tend to be important on a meso to large scale, whereas on a small scale (meters to kilometers), more localized abiotic and biotic factors (tides and currents, geomorphology, predation, competition, etc.) which influence population dynamics translate into factors that influence recruitment success (Table 1). Levin (1994) developed a conceptual model for recruitment of reef related fishes which proposes that settling fish select habitats in a hierarchical manner, suggesting that different attributes of the habitat are selected during different life-history stages. This selection process can have important consequences for the

TABLE 1
Summary of Scale-Dependent Factors that Influence Recruitment Success

Scale	Factor(s)	Reference
Meso to large (tens to thousands of kms)	Climate, freshwater discharge, large scale currents, winds, tides, nearshore prey patchiness	Nelson et al., 1977; Shepherd et al., 1984; Checkley et al., 1988; Peterson et al., 1995; Lazzari et al., 1996; Jenkins et al., 1997; Bradford and Irvine, 2000; Meng, and Matern, 2001; Kimmerer, 2002; Flannery et al., 2002; Doering et al., 2002; Comyns et al., 2003
Small (meters to kms)	Localized tides and currents, geomorphology, predation, competition, prey availability	McGurk 1989; Drake and Arias, 1991; Fogarty et al., 1991; Cohen et al., 1991; Gibson, 1994, Borja et al., 1996; Levin et al., 1997; Edgar, 1999a, 1999b; Rozas and Zimmerman, 2000; Heck et al., 2001

kms = kilometers.

population dynamics of these species. As presettlement nekton are advected across the coastal landscape, they have the opportunity to sample and ultimately select a habitat. The cost and benefits of selection of habitats at various spatial scales should vary with the dispersal ability of an individual. The costs of a continued search for an appropriate habitat type may not be too extreme for pelagic presettlement fishes, whereas the benefits of choosing an appropriate habitat type where it can survive, grow, and reproduce are great. After settlement, a large-scale search for an optimal habitat would be costly because fishes would be required to leave shelter and travel through poor quality habitats. However, the cost of searching on a small scale for the highest quality patch would be low since nekton would never stray too far from cover. The consequences of a poor choice at this scale are probably low compared to the selection of an inappropriate large-scale habitat; the benefits of such a small-scale search are greater because the nekton may be able to locate higher quality food particles or better shelter. Clearly, as Rothschild et al. (1989) indicated, one "... must take into account the nonlinear interactions involved in density-dependent population dynamics and the physical environment at scales of motion comparable with larval scales" when dealing with recruitment issues.

V. ESTUARINE FACTORS OF INFLUENCE

As noted above, much of the research on recruitment tends to be meso to large scale in nature and focuses on factors associated with onshore deposition of larvae. In fact, there are two phases of movement necessary for recruitment into coastal bays and estuaries by estuarine-dependent species: 1) accumulation of larvae in the nearshore zone, and 2) the process of accumulation/attraction of larvae near inlets and bay mouths and eventually passage through them into nursery areas (Boehlert and Mundy, 1988; Cowen et al., 1993; Raynie and Shaw, 1994). Each phase requires distinct physical forcing factors and associated behaviors in order for larvae to reach available nursery habitat. Boehlert and Mundy (1988) provide a conceptual model that considers four habitats sequentially occupied by migrants, including the dominant physical process in the habitat, the stimuli inducing the fishes' behavior, and the dominant activity pattern, all of which determine the transition from one habitat to the next. The process of estuarine recruitment appears to be a continuing one that ultimately depends upon the process of habitat selection once inside the estuary. Thus, once postlarval/juvenile organisms are in the estuary, factors other than transport and retention mechanisms tend to become more important in successful recruitment to nursery habitat. The wide range of habitats present and the new set of stimuli (vegetation, turbulence, prey distribution, substrate type) they provide can lead to selection of shallow areas where flushing from the estuary is reduced or nonexistent. In fact, larval spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*) use, in addition to physical mechanisms like ocean exchange, tidal flows, and net nontidal flows, behavioral mechanisms like diurnal vertical migration which play a major role in recruitment and distribution in the Cape Fear River estuary (Lawler et al., 1988).

The culmination of a series of field and laboratory studies of factors influencing recruitment success of estuarine-dependent weakfish into nursery habitat (Goshorn and Epifanio, 1991; Lankford and Targett, 1994; Grecay and Targett, 1996; and citations within each study), indicated that physicochemical gradients and natural variability of prey along those gradients influence the value of particular estuarine zones as nurseries by affecting the energetics of feeding and growth. Results also indicated a seasonal shift in the location of physiologically optimal nurseries within an estuary which were coupled or uncoupled with prey abundance distribution and theorized to allow for greater or lesser success of estuarine-dependent fishes in general. These results further suggest that the overlap of physicochemical and prey availability gradients noted above reflect nursery ground suitability and the relative contribution of these locations to recruitment success and production. Clearly, controllable laboratory experiments can provide robust and complementary data to field studies concerning the causality and potential of processes such as survival, growth, and reproduction of aquatic organisms subjected to a given environment. The geographic location of settlement from the plankton, annual variation in abiotic variables that drive physiological responses, and/or available prey spectra have been shown to influence variables necessary for successful recruitment (Allen and Barker, 1990; Peterson et al., 1999, 2000a; Rakocinski et al., 2000). Subtle differences among abiotic factors are believed to have significant effects on survival, recruitment, and year-class strength (Houde, 1989; Fogarty et al., 1991; Hinckley et al.,1996; Baltz et al., 1998). Additionally, taxa are known to discriminate among structural characteristics of wetland plants known to be important nursery habitat (e.g., Jenkins and Wheatley, 1998). Finally, in summarizing results of her review on growth of fishes in different estuarine habitats, Sogard (1992) indicated that "assuming that the probability of survival during the nursery period is an increasing function of fish size, plasticity in growth rate implies that the site and habitat into which post-larvae settle from the plankton can indeed have a marked influence on population level dynamics."

These examples suggest that a number of factors play a role in successful recruitment and that these factors may vary with taxa or geographic location, making general patterns difficult to elucidate. However, what is clear is that selection of suboptimal habitats from a gradient of habitat quality leads to reduced growth (Sogard, 1994; Levin et al., 1997) and, by extension, reduced production (Jassby et al., 1995; Demers et al., 2000) but not necessarily to complete loss of a year class. For example, Sogard (1994) noted that for descriptive studies, "growth in the poorest habitat examined was up to 82% lower than in the best habitat." Parrish et al. (1996) determined that because there was a 68-fold higher juvenile abundance of juvenile pink snapper, *Pristipomoides filamentosus*, at premium habitat, it is indicative that such infrequent high-quality habitat is an important (perhaps critical) fishery resource. Because habitat structure changes on various scales, it is reflected in variable levels of production by estuarine organisms (Simenstad et al., 2000). For example, variation in river flow has been shown to influence production of phytoplankton and zooplankton communities associated with critical mesohaline mixing zones along estuarine gradients (Cloern et al., 1983; Kimmerer et al., 1998; Kimmerer, 2002). The position of these important zones shifts toward or away from productive shallow bays on tidal cycles, but also shifts to a greater extent with increased river flow due to precipitation, snow melt, and water releases in regulated systems, and this variability has been associated with survival of the young of fishes like Pacific herring, *Clupea harengus*, striped bass, *Morone saxatilis*, American shad, *Alosa sapidissima* (Stevenson, 1962; Stevens, 1977; Summers and Rose, 1987), and other metazoans (Jassby et al., 1995). In fact, recruitment, growth, and survival of young organisms which vary as a function of river flow, may relate to the organism's position along the gradient or relationship to other habitats (Simenstad et al., 2000).

VI. HABITAT LINKAGES

The maintenance of the complexity and heterogeneity of habitats and their spatial arrangement have been suggested to be vitally important to healthy and productive lotic (Schlosser and Kallemeyn, 2000), lentic (Chick and McIvor, 1994), and estuarine (Irlandi et al., 1995; Irlandi and Crawford, 1997) ecosystems and has been addressed on a theoretical basis (e.g., Wiens, 1989; Dunning et al., 1992; Crowder et al., 2000). Linkages between adjacent marine/estuarine habitats via fish recruitment and/or trophic responses (Parrish, 1989) and nursery and adult habitats (Gillanders, 1997) have been generally documented in tropical systems, although few data exist. In Texas and Louisiana, habitat types may not be equitable (Zimmerman et al., 2000; Minello et al., 2003), as seagrass species and *S. alterniflora* have higher densities of nekton than other habitat types (Minello, 1999). In fact, mean densities of nekton, such as brown and white shrimp, blue crab, and spotted seatrout are higher in *S. alterniflora* marsh edge than seagrass habitats (Minello, 1999). This suggests that the spatial and temporal connectivity of these habitat types may influence overall estuarine productivity and factors that modify this connectivity may further reduce productivity.

Experimental data that support the importance of habitat linkages are from temperate estuarine ecosystems where multiple habitat types (e.g., salt marshes, seagrasses, unvegetated flats) represent habitat heterogeneity at the landscape scale. Irlandi and Crawford (1997) documented that pinfish, *Lagodon rhomboides*, are more than twice as abundant in intertidal marshes adjacent to seagrass beds than in those adjacent to unvegetated subtidal bottom, and that pinfish held in enclosures with both intertidal and subtidal vegetation were, on average, about 90% heavier than fish held in enclosures with intertidal vegetation and unvegetated subtidal bottom. These studies underscore the importance of connectivity among landscape features. Additionally, heterogeneity in the environment results in a mosaic of "rate-determining" habitats (*sensu* Demers et al., 2000) which often have direct and indirect effects on the processes that regulate nekton growth and survival. Reduction in habitat complexity and spatial heterogeneity can thus influence estuarine production.

VII. PUTTING IT ALL TOGETHER: A CONCEPTUAL MODEL

Worldwide, numerous estuarine habitats have been (or are) degraded to some extent, but the functional significance of this degradation is unknown. Because many coastal ecosystems are under increasing pressures from human activities (Vitousek et al., 1997), nekton that use them during part of their life history may be susceptible to declining habitat quality and quantity. In fact, most nekton use multiple habitats through various life stages, and habitat diversity and variability help determine numbers of species and individuals that sustain fisheries production (Greenstreet et al., 1997). To address these issues, a number of approaches have been developed to quantify and predict the influence of salinity, water temperature, or habitat type (Bulger et al., 1993; Hoss and Thayer, 1993; Keleher and Rahel, 1996; Christensen et al., 1997) on species responses and productivity of an area. However, these represent only a part of the overall environment into which species recruit and which may influence successful recruitment. If a more accurate and predictive model of estuarine productivity is to be developed, incorporating dynamic and stationary aspects of the environment as detailed below is necessary. Increasingly, habitat suitability (Christensen et al., 1997; Rubec et al., 1998; Clark et al., 1999; Gallaway et al., 1999), mass-balance models (Walters et al., 1997; Okey and Pauly, 1998), individual-based modeling approaches (Rose, 2000), models of growth rate potential (Demers et al., 2000), and Geographic Information Systems (GIS) environment-based mapping (Keleher and Rahel, 1996; Sabol et al., 2002) are being developed and used to evaluate, manage, and predict future impacts on living aquatic resources. However, these studies are typically based on point estimates of environmental variables and do not incorporate species responses to natural environmental gradients, although the technology to quantify continuous environmental gradients are available (Sieburth and Kester, 1997; Greenstreet et al., 1997; Ross and Ott, 2001; Hains and Kennedy, 2002).

Conservation of living marine resources requires effective management of both fishing effort and the mosaic of habitats across the estuarine landscape that sustain fisheries production. This view broadens management considerations to a whole watershed or ecosystem perspective (Peterson et al., 1995; Botsford et al., 1997). One vital source of recruitment variability is the abiotic environment, "...whether it acts directly or indirectly via their prey or predators" (Neill et al., 1994). Clearly, effective management requires an understanding about how natural and anthropogenic sources of variability in abiotic variables affect fish population dynamics (Rose, 2000). Part of the difficulty of examining large coastal features is our view of the aquatic ecosystem. Environment can be viewed as comprising two components—the physical-chemical (dynamic) and the structural (stationary) (Browder and Moore, 1981). Each has its own influence on nekton which utilize it during part of their life history. Although there is much debate, it is generally believed that survival of nekton depends upon approaching their physiological optima first and then behaviorally searching out the appropriate life-stage-dependent habitat structure for other life requirements (sediment type, food, protection from predators, etc.). In fact, water temperature, salinity, and dissolved oxygen contributed more to growth of juvenile sciaenids in coastal Louisiana than diet and *S. alterniflora* stem density (Baltz et al., 1998). Finally, Meng and Matern (2001) indicated that habitat suitability is controlled by temperature and interannual variations in freshwater flow for native and introduced larval fishes in California.

Salinity has been frequently used as an easily quantified surrogate for the complex estuarine gradient along which nekton segregate (e.g., Jassby et al., 1995; Christensen et al., 1997; Wagner, 1999). Most coastal nekton have various physiological capabilities that may change during ontogeny, which allow them to utilize different habitats within coastal watersheds at various life stages. However, most are not able to utilize the entire range of salinity. Rather, assemblages occur within the coastal watersheds, each being abundant within a relatively narrow part of the salinity spectrum, which in part is driven by the rate of change in salinity as one progresses upestuary (Peterson and Ross, 1991; Christensen et al., 1997). Moreover, coastal fisheries harvest across the GOM is correlated with and varies with local river flow (Deegan et al., 1986). The recruitment success of *M. saxatilis* in California (Stevens, 1977) and *M. saxatilis* and *A. sapidissima* in three rivers of the mid-Atlantic Bight region (Summers and Rose, 1987) is also correlated with river flow. Extremes in freshwater flow in either direction influence fisheries harvest. Shifts in haloclines due to freshwater inflow cause major changes in community structure (Peterson and Ross, 1991; Jassby et al., 1995; Wagner and Austin, 1999) and, potentially, production. Such shifts reduce or eliminate suitable living conditions by placing favorable salinities out of reach of nekton which require habitat not found in the new location.

Nekton in unstable habitats may constantly seek their environmental optima without achieving them because abundance patterns are the result of a composite of environmental factors interacting, rather than a single environmental factor (Neill and Gallaway, 1989; Ryder and Kerr, 1989; Christensen et al., 1997; Rubec et al., 1999). Because the interaction of river water and tides determines the slope of the salinity gradient, both longitudinal and vertical gradients are modified by increased or decreased discharge, frontal passages influencing tides, and storm events (Childers et al., 1990; Fogarty et al., 1991; Sklar and Browder, 1998; Peterson et al., 1995). This direct interaction of river water and tides varies seasonally and tidally, and thus the area of favorable salinity range for a particular species can shift up or down estuary relative to stationary habitat with characteristics like marsh-edge configuration, geomorphology, vegetation type, sediment type, and water depth (Figure 1A). Fishery production may be correlated with the area of favorable habitat (Browder and Moore, 1981) because: 1) growth may be related to available food, and total quantity of available food is the product of food concentration and area; 2) survival and growth rates may be negatively density-dependent; therefore, the larger the favorable area, the higher the survival and growth rates within it; and 3) the smaller the area of favorable habitat, the greater the percentage of juvenile nekton that may use suboptimal habitat, where lower survival and growth rates would be expected. The timing, positioning, and the amount of overlap of the dynamic environmental component with the stationary habitat component may determine the survival and growth rates of juvenile nekton as they pulse into the estuary. If stationary habitat is not limiting or species do not require stationary habitat (anchovies, silversides, menhaden), then only changes in the dynamic component of the environment will influence survival and growth of young nekton. Without a better understanding of habitat distribution relative to water quality variables, including temporal and spatial variability, it is difficult to assess habitat function and thus, the status and trends in habitat quality and productivity. In fact, the direction and extent of environmental variability within estuaries may be a defining characteristic in itself (Boyer et al., 1997).

Overlapping predator/prey spectra, as illustrated by the match/mismatch hypothesis, suggests that annual variation in temporal and/or spatial overlap between larvae and their prey is important to successful recruitment (Cushing, 1990; Gotceitas et al., 1996) and that maximum overlap allows for maximum recruitment success. Additionally, variation in the physical environment can affect growth and survival through 1) disruption of transport to favorable nursery areas, 2) factors related to feeding success, 3) direct mortality through lethal environmental conditions, and 4) indirect effects of all the above (Crecco and Savoy, 1984; Fogarty et al., 1991). Modifying the match/mismatch hypothesis to include environmental variables suggests

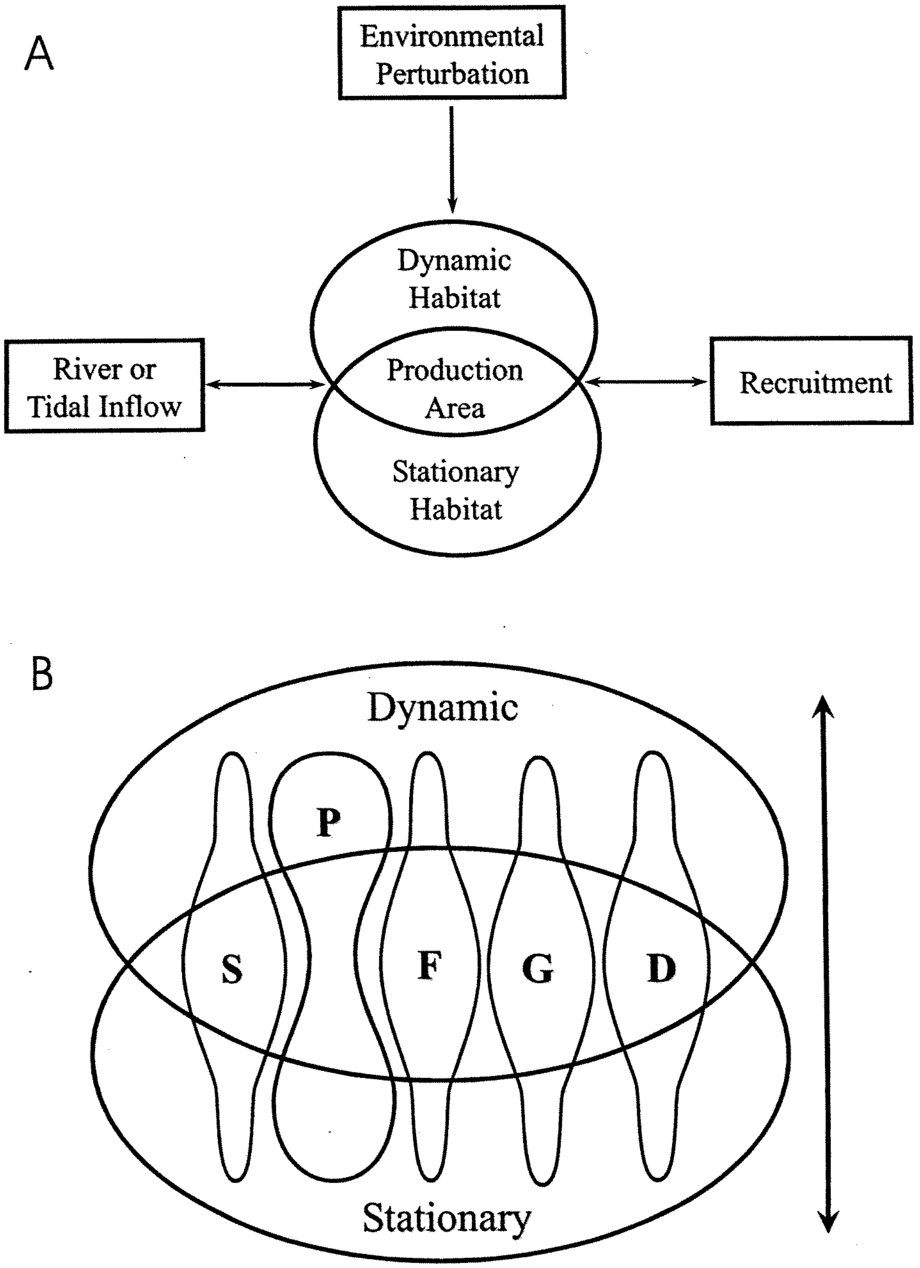

FIGURE 1. (A) Modification of the conceptual model of Browder and Moore (1981), illustrating the connection of dynamic and stationary environmental components and production area in tidal-river estuaries. **(B)** Conceptual model illustrating the connection between the dynamic and stationary environmental components in tidal-river estuaries. Double headed arrow illustrates the potential shift in direction of the dynamic and stationary components of the environment relative to environmental purturbation. This shift in position restricts the area of production and influences the five individual or population metrics presented. P = predation; F = foraging; G = growth; S = survival; D = density.

optimal coupling of these two important elements (i.e., being transported to favorable nurseries with abundant prey) leads to increased recruitment success. This is illustrated by the works of Crecco and Savoy (1984) with American shad (*Alosa sapidissima*) in the Connecticut River, and Childers et al. (1990) with penaeid shrimp in coastal Louisiana salt marsh habitats. First, Crecco and Savoy (1984) noted there was not a significant parent/progeny relationship for American shad even after the recruitment variation due to river flow and water temperature were removed. They found significant correlations between mean river discharge, water temperatures, and total monthly rainfall and year class strength the month of June when most American shad larvae emerge. Furthermore, they determined the mechanism was due to these three abiotic factors, which directly or indirectly affected larval mortality and year-class strength: high June river flows and low river temperatures reduced larval feeding success, survival, and ultimately shad year-class strength (Crecco and Savoy, 1984). The second example is Childers et al. (1990) who determined that climatological forcing like greater-than-average rainfall and ENSO and La Niña events have direct effects on salt marsh flooding, and as a result estuarine production as measured by inshore penaeid shrimp fishery statistics. Most ENSO events cause higher-than-average rainfall, anomalously high water levels, and high marsh inundation regimes associated with large input of fresh water. This input probably decreases juvenile penaeid shrimp habitat horizontally because higher salinity waters are spatially reduced which leads to a decline in shrimp harvest. La Niña events cause low rainfall conditions and increased high salinity areas. However, this may reduce marsh inundation frequency and duration for penaeid shrimp juveniles, causing decline in shrimp harvests due to reduced access to intertidal marsh habitat. Thus, seasonal variability in tides, rainfall, and wind direction and speed, coupled with large-scale climatic variability like ENSO/La Niña events, can influence recruitment of nekton and shift the position of the dynamic component such that it either does not overlap the stationary component or does so infrequently and only to a small degree.

This environment-habitat-production model, based on variation in the spatial and temporal overlap of dynamic and stationary environmental components, attempts to illustrate the linkages between abiotic and biotic conditions along the estuarine landscape that lead to both suboptimal through maximum production areas (Figure 1B). The utility of this conceptual model is that it provides a framework from which testable hypotheses can be extracted and from which much can be learned. It is also useful because tidal river estuaries are driven by freshwater input and tidal exchange mechanisms, both of which can be modified individually or in unison and which can influence the dynamic component of this model. Recently, Flannery et al. (2002) and Doering et al. (2002) have used this dynamic/stationary approach in management of freshwater inflow to estuaries in Florida.

VIII. HABITAT LOSS

Given the conceptual model outlined above, modification of estuarine habitats may lead to the inability to access favorable nursery habitat for estuarine-dependent organisms, which can have negative population effects ranging from reduced recruitment success and fluctuation in year class strength to near-complete failure of a year class, depending on the severity and type of modification. For example, Lawler et al.

(1988) indicated that construction activities at and around inlets can interfere with recruitment rates, recirculation, and behavioral cues that direct recruitment of larval fishes into the estuary. Failure to reach favorable habitat is a common source of annual decrease in settlement of North Sea herring, *Clupea harengus* (Bartsch et al., 1989) and Pacific hake, *Merluccius productus*, off California (Bailey, 1981). Major changes in the trophic structure of estuarine systems can also occur due to natural drought conditions through changes in water color, clarity, salinity, and river flow leading to rapid changes in the pattern of primary production (Livingston et al., 1997). Livingston et al. further postulated that permanent reductions of freshwater flows due to anthropogenic activities by themselves or coupled to natural drought conditions could lead to major reductions of biological productivity in the Apalachicola Bay system.

Habitat loss can be immediate or cumulative (Johnston, 1994). Fishing-related activities can directly or indirectly impact nekton species, through overfishing, bycatch, and reduction of habitat and habitat heterogeneity, and nonfishing-related activities such as impounding, filling, or reducing access to vital nursery habitat impact nekton on a smaller scale (Table 2). Direct habitat loss can occur anywhere along the estuarine axis, and when it does, access by young nekton to vital nursery areas is reduced or eliminated (Kneib, 1997), which may lead to increased mortality, decreased individual growth, and decreased potential production.

Alteration of habitat not only reduces habitat quality for young nekton (Able et al., 1998, 1999), but alters food webs, which can lead to cascading population and community effects throughout the ecosystem (Levings, 1985; Pauly et al., 1998; Lindholm et al., 1999). For example, with loss of SAV in Chesapeake Bay, Ruiz et al. (1993) quantified the distributional shift of many ecologically and economically important small epibenthic crustaceans and fishes to shallow muddy bottom, which they utilized as an alternate refuge habitat. They further speculated that with the

TABLE 2
Summary of Activities and Their Impacts Influencing Fish-Habitat Relationships

Activity	Impact	References
Trawling and dredging	Overfishing, bycatch, habitat loss, reduced habitat heterogenity, sediment composition changes	Dayton et al., 1995; Pauly et al., 1998; Auster and Langston, 1999; Langston and Auster, 1999; Lindholm et al., 1999; Turner et al., 1999; Tegner and Dayton, 1999; Jackson et al., 2001b
Nonfishing, small alterations: marsh filling, bulkheading, piers, docks	Habitat distribution, reduced or eliminated access to marsh, reduced growth, increased mortality, modified settlement	Odum, 1970, 1982; Levings, 1985; Boulé and Bierly, 1987; Suchanek, 1994; Able et al., 1998; Able et al., 1999; Wilbur and Pentony, 1999; Peterson et al., 2000b; Hendon et al., 2000; Rosenberg et al., 2000

worldwide trend in reduction of SAV, significant changes to estuarine ecosystem function, including changes in population and community characteristics of associated fauna, would occur. Fragmented habitat in terrestrial (e.g., Gehring and Swihart, 2003; Rodriguez and Delibes, 2003) and aquatic ecosystems (e.g., Eggleston et al. 1998; Bradford and Irvine, 2000) influence population and community level responses in a number of metazoans. Quantity and fragmentation of suitable habitat influences population size and individual fecundity, and loss of suitable habitat can create a recruitment bottleneck controlling population size (Gibson, 1994; Beck, 1995). Direct alteration can disrupt ecosystem function if habitat becomes fragmented or portions are missing; the habitat structure is incomplete thereby reducing landscape connectivity. Many fisheries are dependent upon habitat and thus fragmented habitat, are unable to function at full capacity, and will adversely affect the sustainability of fisheries (Gibson, 1994; Wilbur and Pentony, 1999; Simenstad et al., 2000; Bradford and Irvine, 2000).

In addition to fishing-related and development/construction-related activities within the estuaries, anthropogenic changes to estuarine hydrology can also influence the environment, the function of EFH, and thus fishery species. For example, modification of the salinity regime, due to dams and reservoir development (reduced freshwater inflow) and dredging to enlarge and deepen coastal ports (increase saline water intrusion), can influence the position of the salt wedge horizontally and vertically along the estuarine axis. This pattern of change has been documented in Texas, Louisiana, Florida, and California, and coupled with annual variability in rainfall (timing and amount) and ENSO/La Niña events, can markedly reposition the salinity regime away from habitat required for freshwater fishes (Peterson, 1988; Peterson and Ross, 1991; Wagner and Austin, 1999) or estuarine-dependent nekton (Peterson and Ross, 1991; Lankford and Targett, 1994; Wagner, 1999). Anthropogenic changes have also been implicated in positioning and maintenance of phytoplankton and zooplankton assemblages (Cloern et al., 1983; Jassby et al., 1995; Kimmerer et al., 1998; Kimmerer, 2002), which are vital prey for myriad young and older fishes.

A better defined relationship between environment-habitat-production as outlined herein would increase our understanding of population and community dynamics, and would be valuable both in theoretical analysis of risk balancing and in predicting the effects of habitat loss or degradation (Sogard, 1994). It would also assist in site selection and optimal spatial proximity of habitats which would be vital in the planning of restoration and mitigation projects (Irlandi and Crawford, 1997), as well as the citing of marine protected areas (Crowder et al., 2000).

IX. SUMMARY

Subtidal and intertidal vegetated habitats are unique components of the estuarine landscape. They provide many vital roles to a many ecologically and economically important fish and crustacean species throughout their life history (Peterson and Turner, 1994; Minello, 1999). However, shallow marsh habitat is also the zone most altered due to commercial and residential development activities. Environmental changes ranging from poor water quality (Livingston et al., 1997) to physical habitat alteration (Suchanek, 1994; Able et al., 1998; Peterson et al., 2000b) influence, directly or indirectly, the organisms that use these habitats during all or part of their life history. These changes can cause serious disruptions of the basic habitat structure, energy flow, trophic ecology, and fish assemblages (Ruiz et al., 1993; Livingston et al., 1997). Indeed, 33 years ago Odum (1970) warned that cumulative impacts and alterations of the estuarine environment would influence estuarine productivity and sustainability. This trend has not been abated (Odum, 1982; Johnston, 1994; Wilbur and Pentony, 1999). These reductions, coupled with food web and community changes due to loss of salt marsh vegetation and seagrass, and increased depth profiles, may alter and further reduce estuarine productivity. Habitat fragmentation is also changing the spatial arrangement of vital habitats along the estuarine axis, such that shifts in the source/sink balance may be occurring. This shift in balance has been suggested by Pulliam and Danielson (1991), Dunning et al.(1992), and Bradford and Irvine (2000) to alter ecosystem health and dynamics and ultimately productivity. To maximize management effectiveness, modelers and managers must recognize and appreciate the biology and ecology of individual nekton and the interactions among populations which lead to productive communities and ecosystems. Understanding linkages between the dynamic and stationary components of the environment focusing on EFH is an important step in the process of developing prudent management strategies in aquatic seascapes.

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