CHAPTER 16

Habitat-Biotic Interactions

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Abstract

Conventional concepts of estuarine and near-shore coastal habitat are generally inadequate descriptions of processes and organisms that respond to habitat variability and change or integrate far larger and more complex "habitat landscapes." In particular, the role of structure within and among habitats, networks through which organisms and critical processes that influence secondary production operate, and the role of estuarine circulation "control point" features in shaping food-web structure and variability are poorly known. In response to these gaps, the Habitat-Biotic Interactions Working Group established as their goal to *identify approaches needed to synthesize a mechanistic understanding of how habitat structure influences estuarine secondary production and food webs.* We recommend eight major steps to enhance synthesis of natural and anthropogenic changes in estuarine production related to habitat-biotic interactions: (1) develop an estuarine habitat classification scheme that relates habitat structure to estuarine production and food-web processes; (2) examine existing long-term data sets to identify the scope and frequency of variability in habitat structure; (3) implement comparative studies of habitat function; (4) develop and link habitat and landscape models that capture the dynamics of biota and process interactions over large estuarine scales; (5) develop indicators of ecosystem habitat integrity, dynamics, and variability; (6) link site-specific field experiments and modeling approaches to scale processes and process understanding across ecosystems and landscapes; (7) apply advanced measurement technologies to give details of distributions and abundances of secondary consumers not now achievable; and (8) link habitat structure to assessment and prediction of resource management scenarios. Addressing ecosystem change in response to habitat structure, as well as the impacts of coastal zone management impacts upon ecosystems, will require innovative

syntheses at much more expanded time and space scales than heretofore considered.

Introduction

To a large degree, the nature and structure of estuarine and coastal habitats control ecosystem productivity and community structure. Resources such as nutrients and light that limit primary production can be extensively influenced by inputs from land and rivers (chapter 4, Fisher et al.; chapter 11, Boynton and Kemp; chapter 2, Howarth et al.; and chapter 3, Vörösmarty and Peterson) or, to a lesser extent, the shelf and open ocean. On the other hand, many of the processes within estuaries and coastal zones that affect nutrient cycling and the conversion of the responding primary production into secondary producer biomass are likely related more to habitat structure. Thus, the source and amount of organic matter at the base of estuarine food webs are determined by diverse allochthonous and autochthonous processes, and prone to considerable spatial and temporal variability, but habitat structure influences the pathways and efficiencies of transfer to consumer organisms at higher levels in the food web. This dichotomy may explain some of the noise and uncertainity inherent in estimating high-trophic-level production based only on nutrient budgets and stoichiometry.

Overall, the scientific view of habitats has until recently been relatively restricted and narrow in terms of taxonomic groupings, ecosystems, and scales (McCoy and Bell 1991). Although we have not conducted a comprehensive review of the literature similar to that of McCoy and Bell, our familiarity with the contemporary literature suggests this myopic view is particularly true for estuarine and coastal ecosystems. For example, the areal extent of specific estuarine and coastal habitats such as marshes and submerged aquatic vegetation has long been used as an index of fish and wildlife production, especially when addressing rearing (nursery) habitats of economically important fish and shellfish, but examination of interactions of these biota *among* habitats over time is infrequent and ecosystem-scale analyses are rare. Although within-habitat linkages to production of higher trophic levels are gradually emerging (such as, fish growth and survival relative to salt-marsh structure), estimates of processes across the estuarine landscape, or comparisons among estuaries with different habitat structures, are wanting. Yet the strength of interactions between biota and their habitat, whether physical (larval transport, aggregation of food particles) or ecological (feeding efficiency, refugia from predators), may be the ultimate determinant of productive capacity *and* composition of consumers at the apex of estuarine and coastal food webs.

Understanding change in the structure of habitat, its influence on fundamental ecosystem processes, responses of habitat-associated biota, and effects

of the anthropogenic components of change is essential to both managing our exploitation of coastal resources and minimizing the impacts on these resources of our occupation of the coastal margin. However, variability and change in biotic interactions associated with natural variation in habitat structure can be difficult to separate from anthropogenic degradation or shifts in habitats. Habitat structure naturally varies and changes over a hierarchy of spatial and temporal scales among different estuaries or within any one estuary. Different types of estuaries reflect dramatically different occurrences and distributions of habitats because of geologic origins and histories and contemporary climatic settings that embrace thousands of square kilometers and years. Within short time and space scales (for example, annual-decadal, meters), variability and change in habitat can also introduce variability in the quantity and quality of productivity at all trophic levels. In what are perceived as the most stable of habitats, such as salt marshes, habitat structure changes over different space and time scales, some of which are relatively predictable (for example, seasonal and successional changes in biota) and others highly stochastic (for example, disturbance events). While scientists have long recognized that variability and change in habitat structure is reflected in variable levels of production by estuarine biota, understanding of the underlying processes is meager. As a result, the diagnostic and, preferably, predictive capability that is necessary to separate natural dynamics in estuarine habitat change and production from changes imposed by anthropogenic effects is insufficient for coastal management decisions. As has been implied already in chapter 12 (Kremer et al.), ecologically complete syntheses require both mechanistic and predictive understanding of the underlying processes that control the composition and production of higher trophic levels. Management of human influences on important ecosystem processes will not improve until interactions between estuarine habitats and dependent biotic resources, such as fish, shellfish, and wildlife, are understood and at least somewhat predictable at larger spatial and temporal scales.

The Habitat-Biotic Interactions Working Group's objective was to *assess how more synthetic approaches should be brought to bear on fundamental questions about the role of habitat structure and variability in estuarine ecosystem processes.* While there is a breadth of valid questions that readily emerge around this issue (table 16-1), the Working Group focused on processes that affected biotic production, and specifically higher trophic level production, which to a large degree defines our socioeconomic and cultural dependence on estuarine ecosystems. We immediately concluded that the ecosystem context of these questions precluded the traditional single-species, single-habitat approach to understanding the role of habitat structure. Understanding the association between estuarine biota and habitats demands life history, physiological, and ecological knowledge of estuarine communities as they interact

TABLE 16-1

Predominance of pelagic vs. benthic food webs?
What estuarine characteristics determines which predominates?
When variable, what controls switching between pathways?
What is the role of benthic-pelagic couplings?

Is biotic diversity related to estuarine productivity?
Do species introductions change food webs?
Does food web efficiency change with biodiversity?

Are there estuarine indicators of estuarine productivity and food web structure and efficiency?
What intrahabitat structural attributes (e.g., edge) influence secondary production?
What landscale-scale features (e.g., habitat linkages, configurations, location) affect secondary production?

How prevalent and variable are regional, extraestuarine influences on estuarine food web structure and production?

What is the importance and variability of higher trophic level (top-down) controls on different descriptors of estuarine biotic communities?
Composition?
Food web structure?
Food web efficiency?
Productivity?
Direct vs. indirect effects?

How have anthropogenic changes in disturbance regimes changed biotic interactions, community structure, and production dynamics?

across the mosaic of habitats that comprise estuarine landscapes. New perspectives and analytical tools are required to gain such an understanding. Consequently, the Working Group formulated the question, What are the effects of habitat structure and change on interactions at ecosystem space-time scales? Implicit in this question are the concepts of (1) strength, (2) variability, and (3) time/space scales of interactions between either individual habitats or overall estuarine habitat structure and estuarine production.

In the Working Group deliberations and the summary below, our goal was to *identify approaches needed to synthesize a mechanistic understanding of how habitat structure influences estuarine secondary production and food webs.* This goal complements the goal of the Linking Biogeochemical Processes to Estuarine Food Webs Working Group (Kremer et al., chapter 12) by examining the relative importance of non-biogeochemical controls on the transfer of organic matter to higher trophic levels. In this respect, the overall "carry-home" message of this volume should ultimately involve integration of recommendations by both of these working groups.

The Concept of Habitat and Habitat Structure

Safriel and Ben-Eliahu (1991) provide a comprehensive definition of habitat that is particularly appropriate to estuarine and coastal ecosystems: "the environment of a community confined to a portion of the landscape," including three components: (1) physicochemical features such as salinity and temperature; (2) resources such as food and space; and (3) interacting organisms other than those functioning as resources, such as predators, competitors, and mutualists. While the concept of habitat is commonly recognized, definitions of habitat structure are more numerous and diverse depending on different taxa and scale viewpoints but may be defined as the arrangement of objects or features in the environment (McCoy and Bell 1991).

Habitat Landscapes

In conventional usage, *habitat* has been defined by the occupation of a particular organism, that is, the locality, site, and particular type of local environment in which an organism is found. However, a broader ecosystem perspective would suggest that habitat embraces any part of the environment on which consumer organisms, directly or indirectly, depend during the estuarine portion of their life histories. Motile consumers (nekton) integrate different habitats in moving among spawning grounds, nursery areas, refugia from predation, feeding zones, and migration routes (Ayvazian et al. 1992). This use of "habitat landscapes" involves multiple scales of space (meters to hundreds of meters) and time (hours to seasons), as aptly illustrated (figure 16-1) for tidal marsh nekton by Kneib (1997). Over a hierarchy of spatial scales within and among habitats, the movement of nekton across the landscape is theorized to account for a "trophic relay" of intertidal primary production that changes over the habitat range and life stage of the nekton (for example, juvenile and adult resident, transient predatory) and habitat (figure 16-2, Kneib 1997). At the extremes of the estuary scale, many species and particularly top-level carnivores account for major fluxes of organic matter and nutrients into or out of the estuarine ecosystem as larvae, juveniles, and adults, with accompanying variability due to both biotic dynamics (for example, population biology, behavior) and physical dynamics (such as river flow and coastal currents; Deegan 1993).

It may be a useful convention to visualize habitats as discrete segments of the environment that fit together to make a place for communities of organisms to persist. These parts include the physical environment (such as substrate provided by plants, sediments, and even organisms, such as oysters), and the

chemical environment (such as temperature, salinity, and dissolved oxygen) and the many organisms (such as plants and invertebrates) that comprise a food web. If portions are missing, the habitat is incomplete or damaged and unable to function at full capacity or be sustainable. Similarly, adopting a life history and ecosystem perspective compels ecologists to examine habitat-biotic interactions among habitats across habitat landscapes. Given the multidimensionality of factors defining habitats, we can conceptualize habitats as having

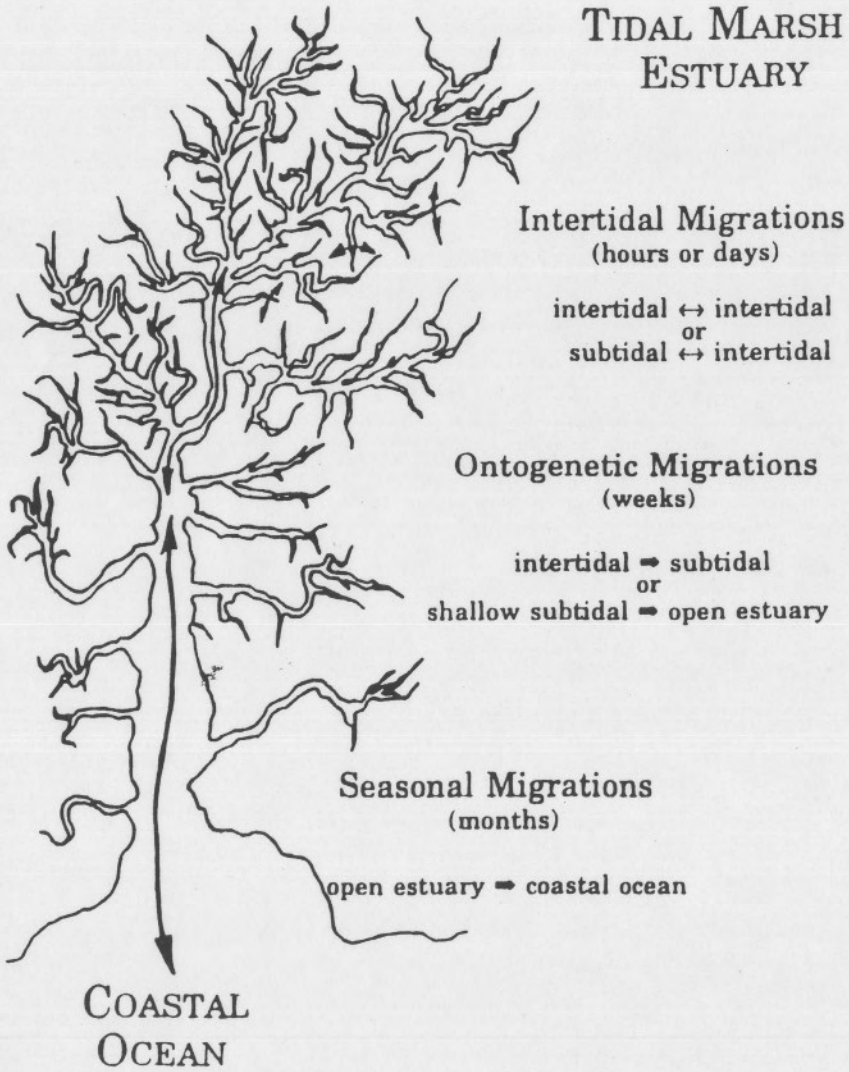

FIGURE 16-1 Nekton movement among estuarine tidal-marsh habitats demonstrating range of short-term (behavioral movement between intertidal and subtidal) to longer-term (ontogentic [life-history] and growth-related) space and time scales (from Kneib 1997, used with permission).

three primary components: (1) complexity; (2) heterogeneity; and (3) scale, where complexity defines the individual habitat elements, heterogeneity the complex of different habitat elements (and habitats), and scale the scale at which they are integrated (figure 16-3). An important contribution to habitat structure is often the "architectural" influence of the organisms themselves, exemplified by the communities that develop around large, hard-shelled

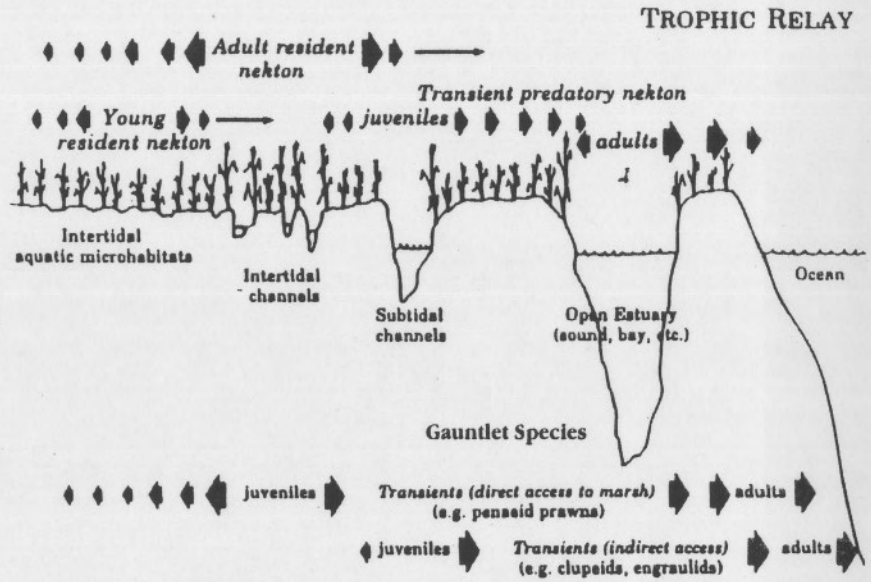

FIGURE 16-2 Trophic relay of intertidal marsh production involving different life stages of resident and transient nekton across habitat landscapes (from Kneib 1997, used with permission); gauntlet species are nekton, particularly forage fishes, whose juveniles encounter a gauntlet of predators during their large-scale migrations from the spawning ground to the estuary and back.

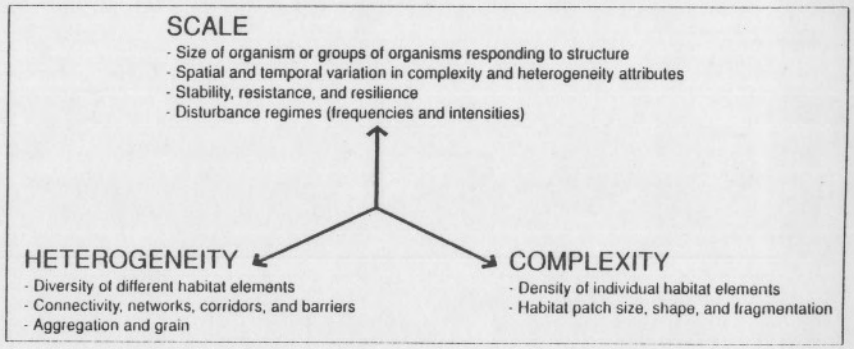

FIGURE 16-3 Components of habitat structure. Modified from McCoy and Bell 1991.

bivalves such as oysters and mussels that form reefs, and tubes, burrows, and castings of soft-substratum macrofauna such as polychaetes and bivalves (Sebens 1991).

The relationship between an organism and its habitat is also highly dependent on the organism's taxonomy, size, and trophic status. The habitat of a protozoan, which might entirely encompass the sphere of an estuarine aggregate <50 μm in diameter, is vastly different from striped bass habitat, which includes several different locations within estuaries as well as near-coastal waters outside the estuary. From an ecological perspective, however, there can be strong linkages between the protozoan and striped bass because the striped bass may depend on a food-web pathway initiated by the protozoan.

In defining habitat, the primary descriptors have been physical location, geomorphology, and biological features because these provide a convenient organizational typology. Thus, a habitat is most directly described by its position along a salinity gradient, tidal flooding regime (or tidal elevation as a indicator) substrate type, energy (wave, current) exposure, and dominant biological components, as demonstrated by the U.S. Fish and Wildlife Service's National Wetland Inventory (NWI; Cowardin et al. 1979). However, the biological components often become the primary descriptors, such as marshes, tidal forested swamps, oyster reefs, kelp beds, eelgrass meadows, mangroves, and intertidal and subtidal mudflats or sandflats. Less obvious, but equally important, examples are structural features inherent in different types of estuarine circulation, such as tidal fronts separating different water masses or plumes of low-salinity water produced by large rivers (color plate 11).

Physicochemical characteristics that determine physiological and behavioral responses of estuarine biota also delimit organisms' habitats. Environmental properties such as temperature, salinity, and dissolved oxygen greatly influence the scope of use of habitats, especially where extreme variation occurs, as in most intertidal habitats. Evolutionary and real-time responses limit organisms' recruitment, foraging, and general movement. This is illustrated in the estimate of growth potential of striped bass in Chesapeake Bay, as estimated by bioenergetic models using temperature, prey density, and prey size distributions (Brandt and Kirsch 1993; see also figure 15-5 in this volume).

Connectivity and Control Points

Landscape features that link habitats influence the flux of dissolved and suspended constituents and the management of organisms. Networks and corridors, such as dendritic tidal rivulet and channel systems, play particularly important roles because they link a geohydrologic continuum of habitats with varying geochemical functions (for example, constitute sinks or sources

of nutrients and dissolved and particulate materials; Dame et al. 1992) and provide corridors of access for nekton foraging along the marsh edge and seeking refuge within marsh vegetation (Rozas and Odum 1987; Rozas et al. 1988; Minello et al. 1994; Kneib 1997). The continuum of habitats and linking corridors become particularly important to anadromous and catadromous nekton species, such as salmon, which must traverse the entire estuarine gradient at several stages in their life history (Simenstad and Cordell, in revision). Therefore, habitat structure at the ecosystem scale encompasses the configuration, and arrangement and connectivity, of habitat elements that typify most estuaries (figure 16-4).

Unique water-column features of estuarine hydrodynamics also contribute to habitat structure. In addition to tidal fronts, where concentration of plankton and other food particles provide a distinct foraging interface for fish and seabirds, circulation "control points" along the estuarine gradient can be sites of intense geochemical and biological activity (color plate 12). Control points may be described as circulation discontinuities that are caused by focusing of advective and diffusive processes. These locally intensify chemical and biological interactions either directly because of circulation (for instance, upwelling) or indirectly because of organisms' volitional responses to the feature (such as fish and bird foraging). One of the better examples of such control points is

FIGURE 16-4 Complex estuarine continuum of forested watershed, freshwater tidal marsh, salt marsh, creeks and pannes, Plum Island Sound (Massachusetts), barrier beach, maritime forest, and the Atlantic Ocean.

estuarine turbidity maxima (ETM), where residual circulation and other effects produce a region of intense trapping and aggregation of inorganic and detritus particles, zooplankton, and larval fish, and high bacterial activity (Uncles and Stephens 1993; Baross et al. 1994; Bernat et al. 1994; Jay 1994; Simenstad et al. 1994a, 1994b; Morgan et al. 1997; Crump and Baross 1996). ETM have been shown to account for a disproportionally high contribution to the food web in the Columbia River estuary (Simenstad et al. 1990), and to be associated with recruitment processes of anadromous fish and blue crab growth in Chesapeake Bay (Boynton et al. 1997). Because of the intense concentration of material and activity at control points, they likely form an important lateral extension of shoreline habitats, such that consumers in peripheral shallow and wetlands benefit from the proximity to ETM through increased food resources.

Habitat Variability, Natural and Anthropogenic Change

Habitat variability is a consequence of changes in geomorphology (water, circulation, basin morphology), watershed, and water quality (light attenuation, chemistry), and biological characteristics (the structural effects of organisms such as submerged aquatic vegetation, oysters, and the like) influencing estuarine and near-coastal environments. A knowledge of these three factors and their influence on food-web pathways is required to assess levels, efficiency, and variability in estuarine productivity. Estuaries vary in their fundamental characteristics that relate forcing (for example, tidal, river flow, wind) to physical processes (circulation and sediment transport; see Jay et al., chapter 7). Some of the variables from estuary to estuary that can affect food webs and productivity are water inputs, tidal influences, water and particle residence times, stratification characteristics, and basin morphologies. For example, the Columbia and Chesapeake estuaries, while sharing some common estuarine features, are notable for their distinct differences in habitat structure, which result in contrasting levels and quality of productivity.

Numerous documented and anecdotal observations of changes in estuarine productivity are associated with changes in habitat. However, while we have considerable knowledge of productivity and food-web processes in some estuarine systems, we lack synthetic ability to extend that knowledge to other estuaries with similar or different habitats. Many obvious effects of major habitat changes introduced by humans, such as deforestation, wetland loss, damming of rivers, increased nutrient loading, and introductions of exotic species, are known for many estuaries. Comparably dramatic natural changes, such as from hurricanes (Ruzecki et al. 1976), have also been described. More subtle, indirect effects of habitat change that may occur progressively or incrementally over a variety of time and space scales are less well known and quite often are indistinguishable from changes due to natural sources. Furthermore, there have been very few comparisons of habitat change across diverse estuarine ecosystems that lead toward a general understanding of the consequences to estuarine food webs.

Acute Habitat Change

Acute habitat change tends to result from direct impacts, usually intense natural disturbances (for example, hurricanes, freshwater flooding) or activities by humans (such as dredging or filling). These can cover extensive areas, as in hurricane effects (Chabreck and Palmisano 1973), but often do not result in a permanent change in estuarine processes. The persistence of natural estuarine processes facilitates natural recovery of the pre-disturbance habitat structure. However, both continual removal of estuarine habitat and alteration of natural physical and geomorphic processes results in a comparatively permanent shift in production. Maryland and Connecticut have lost 74% of their estuarine wetlands, California, 91% (Dahl and Johnson 1991). Dredging, diking, and filling of emergent wetlands alone is principally responsible for a loss of greater than 94% of San Francisco Bay's historic marsh habitat (Nichols et al. 1986), and an average of 42.5% of these important, highly productive habitats have been removed from Pacific Northwest estuaries, with many having lost over 60% (Bortleson et al. 1980; Boulé 1981; Boulé et al. 1983; Boulé and Bierly 1987). Dredging of canals and navigation channels alone has caused a direct loss of ~16% (12,000 ha) of Louisiana's coastal marshes (Turner and Cahoon 1988; Boesch et al. 1994). The most recent analysis of *Status and Trends of Wetlands in the Conterminous United States* (Dahl and Johnson 1991; Dahl and Allord 1997) suggests that these dramatic rates of intertidal habitat loss are declining, but between 1985 and 1995 an alarming 3,760 ha of total estuarine wetland habitat, and 734 ha of estuarine subtidal habitat, disappeared.

Chesapeake Bay has suffered significant habitat losses and modifications that impact fisheries productivity and have diminished quality of bay habitats for overall biological productivity. Early declines in anadromous fish (shads, river herrings, striped bass) were a consequence of blockages and dams on spawning tributaries (Hildebrand and Schroeder 1928), but later declines that became precipitous in the 1970s probably were attributable to multiple causes, including fishing, habitat loss, and declines in habitat quality. For example, 2.5% of the wetlands in the bay watershed were lost during the period 1982 to 1989 (Tiner 1994). Although not easily assignable to any specific cause, declines in fisheries productivity followed Hurricane Agnes in 1972 and were concurrent with increased nutrient loadings, losses of seagrass

meadows, and concomitant effects on habitat quality. American shad, once the object of the most valuable fishery in the bay, dwindled to levels that required a moratorium on fishing (Anonymous 1989). Striped bass stocks recovered under greatly reduced fishing mortality, demonstrating that habitat deterioration alone was not the cause of the species' collapse (Richkus et al. 1992). Oysters have declined to disastrously low levels in the bay. While the causes are debatable, heavy fishing, destruction of habitat by the fishing process, siltation of oyster beds, and the prevalence of disease in the stressed, remnant stock (Rothschild et al. 1994) indicated that habitat destruction was one significant contributor to the disastrous decline. The role of seagreasses in fisheries productivity has not been clarified for Chesapeake Bay, but recent signs of modest recoveries in bay seagrasses (Anonymous 1995) are viewed with optimism by ecologists and fishery managers concerned about the bay's fisheries resources.

Subtle Habitat Change

Subtle, long-term habitat changes can involve more chronic or indirect mechanisms, including (1) degradation of water quality from eutrophication (for example, increased areas and persistence of hypoxia/anoxia); (2) loss/reduction of sediment sources (such as shifting from accretion to erosion regimes in marshes); (3) shifts in estuarine circulation (for example, salinity distribution) due to river diversion and regulation; (4) coastal subsidence and/or sea-level rise; (5) disturbance or removal of keystone species or other critical habitat components by fisheries or other mechanisms (such as disease), and (6) introductions and expansions of exotic species. Compared to acute habitat changes, these more subtle, chronic changes typically produce nonlinear and often highly complex responses by estuarine biota that are often difficult to distinguish from natural fluctuations.

These more subtle anthropogenic influences can significantly alter the processes that control higher trophic level production independent of obvious structural changes such as measurable loss of habitat. A well-documented example of this is the effect of eutrophication on fish production in submerged aquatic vegetation (SAV) habitats (Deegan and Buchsbaum in press). Eutrophication increases algal growth (plankton, epiphytes, and macroalgae) preferentially over vascular plants. This change in plant community affects food acquisition and survivorship of juvenile fish that use the SAV habitat as a critical nursery area. Food webs are altered as the invertebrate community responds to changing plant assemblages, in part as invertebrate susceptibility to predation by small fishes declines as increased algal cover provides more refuge. The declines in vascular plant density, biomass, height, and health increase the susceptibility of small fish to predation. The integrated result of these shifts in habitat primary production and architecture is a decline in the food chain in the extent and distribution of submerged aquatic vegetation

abundance and growth of small fish (Deegan and Buchsbaum in press). These changes occur long before the SAV habitat disappears.

More subtle differences in the character or quality of a habitat may also be reflected in varying production. The growth of juvenile fish, for example, is demonstrably different in different estuarine habitats (see Sogard 1992, 1994; Sogard and Able 1992). Recruitment growth and survival that varies as a function of river flow may relate to control-point dynamics and position, or relationship to other habitats (such as nurseries; Stevens 1977).

Examples of Documented Habitat Changes and Estuarine Responses

Examples of some of the better-documented changes in estuarine function associated with habitat alteration include (1) impacts of major water withdrawals from river flow into San Francisco Bay, the Gulf of Mexico, and the Sea of Azov; (2) construction and operation of the High Aswan Dam; (3) eutrophication of Chesapeake Bay; (4) extensive colonization of exotic species in San Francisco Bay; and (5) a complex combination of natural and anthropogenic changes in the Mississippi River delta.

River inflow to estuaries fluctuates naturally and both drought and flood extremes alter habitat-associated production and food-web relationships. For example, drought effects on fish production, caused primarily by changing optimum habitat utilization, has been documented to alter secondary productivity and trophic structure (Austin and Bonzek 1996; Livingston et al. 1997). However, anthropogenic diversion and regulation of river flow can impose far-reaching impacts, over diverse time scales, to fundamental habitat-structuring processes in estuaries that, unlike natural fluctuations, may be difficult to reverse (Simenstad et al. 1992). Alterations of the natural hydroperiod can affect estuarine circulation on different time and magnitude scales, ranging from short-term (diel, peak power-generation cycles) to longer-term (seasonal or interannual) changes. As a result, longitudinal and vertical estuarine habitat structure is altered by changes in mixing and salinity regimes, and the position and dynamics of control-point features altered. Truncated flooding can reduce sediment and nutrient inputs to estuarine wetlands. Reduction in flooding reduces disturbance frequency and intensity in modifying estuarine geomorphology, allowing wetlands and other intertidal habitats to evolve toward higher successional stages. Loss of riparian habitat flooding may also reduce the flux of organic matter flux to the estuary.

Even partial loss of freshwater flow imposes stresses on natural estuarine habitat functions. Losses of 40–60% of the freshwater flow (and higher diversions during high flow periods), and 60–75% of the sediment input, into north San Francisco Bay have impacted the production of estuarine biota, particularly those associated with the critical mesohaline mixing zone and estuarine

Action Items and Recommendations

Need for Ecosystem Approach

Among the nine issues that the National Research Council (1994) identified as posing significant threats to the integrity of coastal ecosystems, five (eutrophication, habitat modification, hydrologic and hydrodynamic disruption, introduction of nonindigenous species, global climate change and variability) directly involve the issue of habitat changes on estuarine secondary production. Recent emphasis placed on "essential fish habitat" under reauthorization of the Magnuson-Stevens Fisheries Act further illustrates acknowledgment of a direct link between fisheries production and the integrity of aquatic habitats. However, estuarine science has rarely dealt in a diagnostic or predictive manner with assessing change, either within-habitat variability over a landscape, or much less, the consequences to sustainable resources. Continued investment in habitat-specific applications of models, comparisons, and experiments will not alone provide the scientific and management community with the information needed to scale the effects of habitat change on production to the level of estuarine ecosystems. This "ecosystem approach" requires understanding of the fundamental linkages among ecosystem components, biological responses to physical and geochemical processes, rates and variability of these underlying processes, and the effect of disturbance and other modes of ecosystem change. But even more holistic approaches are required, especially those that approach habitats as landscapes and enable the discrimination of natural from anthropogenic change. Inquiry into the importance of estuarine habitat structure to production processes requires a highly integrated understanding of fundamental physical, chemical, and biological processes derived from the iteration between data and synthesis (figure 4-2, Fisher et al., chapter 4).

Recommendations

The Working Group recommends eight major initiatives that would advance syntheses of natural and anthropogenic changes in habitat-biotic interactions on estuarine production:

1. develop an estuarine habitat classification scheme that relates habitat structure to estuarine production and food-web processes;
2. examine existing long-term data sets to better define variability in secondary productivity as a function of change in habitat structure and integrity;
3. implement comparative studies of habitat function and change among and within estuaries;

4. develop and link habitat and habitat landscape models;
5. develop indicators of ecosystem habitat integrity, dynamics, and variability;
6. link site-specific field experiments and modeling approaches to scale processes across ecosystems and landscapes;
7. apply advanced measurement technologies to give details of distributions and abundances of secondary consumers not now achievable; and
8. link habitat structure to assessment and prediction of resource management scenarios.

The focus of these initiatives is to develop and synthesize information on estuarine habitat-biotic interactions that can be employed to compare habitat differences and production processes in divergent estuarine ecosystems.

1. Develop an estuarine habitat classification scheme that relates habitat structure to estuarine production and food-web processes. Any synthetic approach to assessing habitat-biotic interactions requires an estuarine classification scheme that incorporates physical, geomorphic, and geochemical attributes of habitats that have ecological significance (Jay et al., chapter 7). Systematic habitat classification is particularly important for ecosystem comparisons. With the exception of the recent emergence of the hydrogeomorphic (HGM) system (Brinson 1993), estuarine habitat classification has not progressed significantly since development of the estuarine system structure under the Cowaradin et al. (1979) National Wetland Inventory system. While HGM incorporates more geomorphic attributes, it does not classify variability in within- or among-habitat structure.

An ecosystem- or habitat landscape-based classification scheme should utilize diagnostics of both within-habitat and interhabitat processes, such that we can progress beyond the persistent assumption that biotic production is linearly related to habitat area. Little attention has been paid to landscape characteristics, such as position along the estuarine gradient, connections between similar habitats, and habitat patch size and shape. Furthermore, such an estuarine habitat classification scheme needs to be placed in a hierarchical context within a higher-order classification of the type of estuary and watershed (Jay et al., chapter 7).

2. Examine existing long-term data sets. Within-estuary fish and macroinvertebrate catches need to be examined and compared in order to understand the variability in secondary production across different types of estuaries with different habitat composition and extent. Most of the "controls" on various estuarine processes are actually the products of interactive

processes. For example, high river discharge has a different effect in estuaries with vast expanses of salt marsh as compared to estuaries with large, shallow, unvegetated areas. We need to develop broad-scale relationships between multiple and interconnected habitat configurations and measure secondary production over sufficient periods to capture the effects of interannual variability.

Similarly, covariability relationships between growth and survival of consumer life-history stages and their residence in control-point and other habitat features should be explored relative to the temporal and spatial dynamics of these features. For instance, the position and intensity of tidal fronts and estuarine turbidity maxima vary in part as a function of river-flow forcing. The recruitment and year-class strength of fish and macroinvertebrates that are specifically associated with these habitat features, or occupy adjacent habitats, could relate directly or with some predictable lags to variation in intra- and interannual river flow.

3. Implement comparative studies. Cross-system comparisons of estuaries with different habitat structure, which may be related to inherent differences in land-margin characteristics (see first recommendation, Jay et al., chapter 7) as well as anthropogenic changes, provide one of the most powerful mechanisms to explain differences or changes in estuarine production processes. In particular, variability in fish and shellfish production (for instance, commercial catches) that is evident in comparisons of nutrient loading (Nixon et al. 1986; Boynton et al. 1995) may be elucidated further by relating both the quantity and quality of habitats that are known or suspected to affect the survival and production of fisheries species. Other system contrasts that would be relevant to habitat-biotic interactions include freshwater inflow regimes; quantity and quality of organic matter fluxes; estuarine circulation features (such as estuarine turbidity maxima); and invasions and changes in prominence of exotic species. One example of an insightful comparison is the inherent difference in processes dominating estuarine food webs, or in phase shifts among dramatically different processes, relative to the role of physical and geomorphic characteristics of different estuaries. Dame (1996) illustrated this relationship between estimated estuarine residence time and bivalve clearance rates that discriminates where suspension feeding does or does not regulate system trophic structure (figure 16-5).

4. Develop and link habitat and habitat landscape models. Recent technical and conceptual developments in spatially explicit modeling (see Demers et al., chapter 15) provide the means to relate habitat structure to estuarine processes. It is now feasible to incorporate habitat-specific submodels into

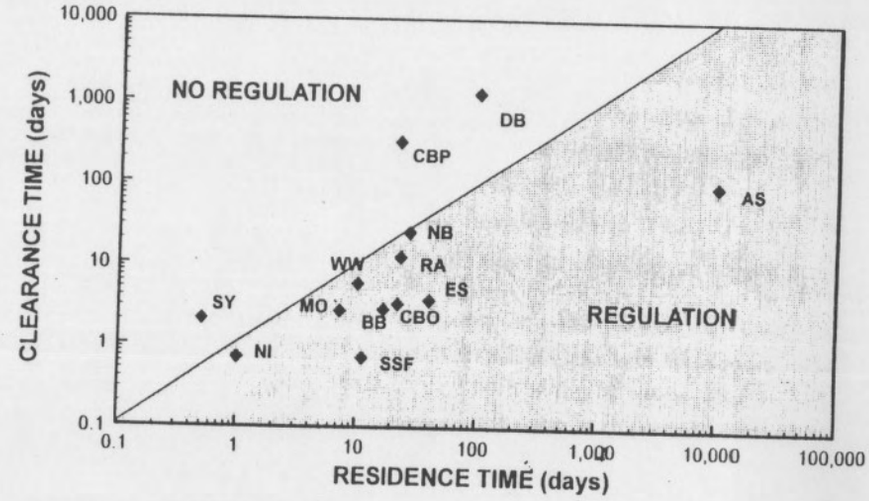

FIGURE 16-5 Relationship between bivalve clearance time and residence time, and potential for suspension feeding to dominate trophic structure, in a number of estuaries (from Dame 1996, used with permission from CRC Press); AS = Asko, Baltic Sea; BB = Bay of Brest; CBO = Chesapeake Bay, past; CBP = Chesapeake Bay, present; DB = Delaware Bay; ES = Eastern Scheldt; NB = Narragansett Bay; NI = North Inlet; MO = Marennes-Oleron Bay; RA = Ria de Arosa; SSF = South San Francisco Bay; SY = Sylt; WW = Western Wadden Sea.

two- and three-dimensional hydrodynamic models and other large ecosystem models to explicitly incorporate relevant space and time scales. Although still complex and requiring extensive code and input data, such ecosystem models can be designed to address fundamental questions about long-term, subtle and nonlinear responses of estuarine biota to habitat change. Examples of synthesis approaches that are amenable to spatially explicit ecosystem models include (1) examining scenarios or comparing differences in estuarine structure at the estuary or watershed scale; (2) testing hypotheses concerning whole-ecosystem processes such as benthic-pelagic couplings; (3) modeling natural experiments such as the impact of different nutrient-loading regimes on bottom-up (verses top-down) effects; (4) evaluating the significance of taxonomic or functional group changes by testing the sensitivity of model predictions to different species, size, or functional groups; and (5) predicting habitat and associated biotic responses to changes in circulation (such as residence time and stratification/mixing) due to river inflow manipulation.

5. Develop indicators of ecosystem habitat integrity, dynamics, and variability. Despite the plethora of paradigms about the importance of estuarine habitats to secondary production, particularly fisheries and aquaculture resources,

estuarine habitats and the resulting ecosystem responses. The use of "ecological performance indices" such as posed by Done and Reichelt (1998), relating the temporal and spatial scale and intensity of fishery disturbance to habitat distributions and successional stages, presents one such approach to evaluating the alternatives between degraded and desirable ecosystem states.

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