

SYNTHESIS OF LINKAGES BETWEEN BENTHIC AND FISH COMMUNITIES AS A KEY TO PROTECTING ESSENTIAL FISH HABITAT

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ABSTRACT

Several essential fish habitats lack the protections necessary to prevent degradation because of failure to integrate the scientific disciplines required to understand the causes of the degradation and failure to integrate the fragmented state and federal management authorities that each hold only a piece of the solution. Improved protection of essential habitat for demersal fishes requires much better synthesis of benthic ecology, fisheries oceanography, and traditional fisheries biology. Three examples of degraded habitat for demersal fishes and shellfishes are high-energy intertidal beaches, subtidal oyster reefs, and estuarine soft bottoms. In each case, both scientific understanding of and management response to the problem require a holistic approach. Intertidal beach habitat for surf fishes could be protected by constraints on the character of sediments used in beach nourishment and restriction of nourishment activity to biologically inactive seasons. Subtidal oyster-reef habitat for numerous crabs, shrimps, and finfishes could be protected and restored by reduction of nitrogen loading to the estuary and elimination of dredge damage to reefs. Estuarine soft-bottom habitat for demersal fin- and shellfishes could also be protected by reduction of the nutrient loading of the estuary, which could prevent associated problems of nuisance blooms and low dissolved oxygen. Although a broad general understanding of the nature of habitat degradation exists for each of these three examples, the interdisciplinary science needed to sort out the separate and interactive contributions of all major contributing factors is incomplete. Adopting the holistic approach embodied in the principles of ecosystem management sets a course for addressing both the scientific inadequacies and the management inaction.

Management of natural resources has been undergoing a fundamental paradigm shift away from exclusive consideration of individual resources as commodities and toward a more holistic evaluation of how the resources interact with the broader ecosystem. This approach, often termed ecosystem management, is distinguished from more traditional management approaches by its appreciation of how components of the ecosystem interact to affect the resources of value, its explicit commitment to sustainability, and its adoption of accountability in the form of adaptive management (Christensen et al., 1996; Fogarty and Murawski, 1998). The application of principles of ecosystem management to land management has advanced beyond the conceptual stage (e.g., Grumbine, 1994), but for marine ecosystems the scientific basis for their practical application remains to be developed (National Research Council, 1996; Botsford et al., 1997). The new mandate for defining and protecting essential fish habitat in the 1996 Magnuson-Stevens Fisheries Conservation and Management Act increases the urgency of progressing with ecosystem approaches to fisheries management.

Habitat for demersal fishes by definition includes the seafloor and its biotic assemblages. Demersal fishes use seafloor benthic communities as protection and as prey dur-

ing critical phases of their life cycles. These benthic communities in turn reflect the integrated contributions of processes and events in the overlying water column and in the drainage basin that feeds into it (Warwick, 1993). The open nature of marine and estuarine systems implies that their functioning is affected not only by local aquatic events but also by terrestrial activities, especially those that release materials into the watershed or atmosphere. Benthic habitat has been greatly degraded and even destroyed by direct effects of dredging, trawling, longlining, and dynamiting in the pursuit of fish (Dayton et al., 1995; Roberts, 1995; Thrush et al., 1998). The more indirect influences of alterations in the watershed are less well understood but arguably as important. Proper management of essential habitat for demersal fishes, especially in nearshore marine environments and in the estuary, requires a synthesis of impacts of the full suite of these diverse activities on benthic communities and the consequences of those activities for fish production.

Here, by exploring three underappreciated examples, we show how the community of invertebrates on the seafloor integrates and reflects impacts of various human activities. We show how these changes in the seafloor benthos endanger sustained production of demersal fishes, and we identify the areas of future research that are most critical to evaluation of their significance. We use three examples, chosen because of their wide applicability and the differing responsibilities and challenges each represents for management. We also discuss the implications of the natural science for how management institutions should be altered to approach an ecosystem basis for protecting essential fish habitat. Achieving ecosystem-based management requires not only holistic technical and scientific information but also holistic management that cuts across and integrates responsibilities of multiple management agencies, including traditional federal and state responsibilities. Each of our examples—exposed sand beach habitat, subtidal oyster-reef habitat, and estuarine soft-sediment habitat—demonstrates the critical need for synthesis of agency responsibilities to provide the ecosystem management necessary to protect (and now restore) the function of essential fish habitat.

THE INTERTIDAL SAND BEACH HABITAT

Along developed shorelines, beach erosion has prompted a variety of responses intended to protect the investment in buildings and infrastructure behind the beach. A recognition that structural ('hard') solutions to beach erosion, such as seawalls and jetties, have serious unintended consequences has led enlightened coastal managers to permit only 'soft' solutions to beach erosion, namely beach nourishment and bulldozing (Walton and Sensabaugh, 1979; Pilkey and Wright, 1989). The physical disturbance to the intertidal beach caused by replacing eroded sands during either nourishment or bulldozing is intense and has great potential for degrading the biological (and socioeconomic) value of the intertidal beach as fish and wildlife habitat. The beach represents essential habitat for several species of fish, acting either as juvenile nursery or as feeding grounds for many life-history stages (Brown and McLachlan, 1990). Along the southeast coast of North America, the beach habitat provides the essential prey resources for pompano (*Trachinotus carolinus*), Gulf kingfish (*Menticirrhus littoralis*), and summer flounder (*Paralichthys dentatus*) (Hackney et al., 1996). A loss of the dominant benthic prey, mole crabs (*Emerita* spp.) and bean clams (*Donax* spp.), on the intertidal beach would remove the necessary forage resources for these commercially and recreationally valuable fishes. Because sea

Table 1. Impacts of beach nourishment on beach habitat.

(1) Direct burial and mortality of beach invertebrates (forage base for consumers)
(2) Modification of sediment character inhibiting recolonization by invertebrates
(3) Increased turbidity
(a) During the project, affecting survival of suspension-feeding invertebrates at some distance and affecting feeding efficiency of visually orienting nearshore pelagic fishes
(b) After the project, long-term turbidity from erosion of fine sediments and mud balls
(4) Loss of prey for surf fishes and shorebirds
(5) Reduced suitability of back beach for sea-turtle nesting
(6) Destruction of dune plants that stabilize shoreline and build dunes

level is likely to rise at increasing rates in the wake of global warming (National Research Council, 1987), the demand for beach nourishment and bulldozing seems likely to grow. Such soft solutions to beach erosion have a limited life time of only a few years, requiring the frequent, repeated disturbance of the beach habitat (Leonard et al., 1990). More and more beaches may be subjected to almost continuous nourishment to maintain the position of the shoreline in the face of rising sea level.

Reviews have summarized the effects of beach nourishment on the ecology of this system (Nelson, 1989, 1993; Hackney et al., 1996), but ecological work evaluating impacts of beach bulldozing is limited (but see Peterson et al., in press). Beach nourishment affects the function and value of fish habitat (Table 1) (1) by burying and killing essentially all of the macroinvertebrates in the intertidal zone; (2) potentially by altering the character of the sediments so as to affect the rate of recolonization and the ultimate community composition and species abundances after recolonization; and (3) by inducing turbidity in the nearshore water column, which kills suspension-feeding benthic animals over some distance beyond the deposition site (Reilly and Bellis, 1983) and affects the water-column habitat by reducing ability of visual predators to detect their prey (see, e.g., Benfield and Minello, 1996). Bulldozing can also kill resident benthic invertebrates of the intertidal beach, while in addition steepening the beach profile and altering the sedimentology, compaction, and nature of the sands on the deposition sites of the primary dune (Wells and McNinch, 1991; Peterson et al., in press). Although some partial assessments of the effects of beach nourishment and bulldozing on benthic invertebrates have been conducted, the research done to evaluate the indirect consequences to the functioning of the essential habitat for surf fishes is grossly incomplete.

A study of effects of beach nourishment and bulldozing on the same beach in North Carolina illustrates the differences in short-term ecological implications between the two (Peterson et al., in press). Beach nourishment using finer but still legally accepted sands (3.67 vs 2.33 Φ) from maintenance dredging of the Intracoastal Waterway was conducted at two separate sites on Bogue Banks from early March through 24 May. Sampling in early to mid-July of that same year revealed densities of both *Emerita talpoida* and *Donax* spp. to be 86–99% lower on nourished beaches than on control shores nearby. The summer season is the period when the intertidal beach serves as the feeding grounds for surf fishes. Although fishes were not directly studied, depression of abundances of the two prey that comprise the vast majority of their summer diets is likely to have adversely affected the pompano, kingfish, and summer flounder. The bulldozing (performed in April and assessed in late July–early August) had less impact on the beach macroinvertebrates. The major effect was a 55–65% reduction in ghost crabs in response to alteration of the

Table 2. Factors that determine the degree of habitat degradation caused by beach nourishment on high-energy sand beach.

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- (1) Season of disturbance (because biological occupation is restricted to warm season)
 - (2) Character of sediments used
 - (a) Sand grain size (should not be smaller than that of natural beach)
 - (b) Shell content (should be low)
 - (c) Mud ball content (should be low)
 - (d) Toxic chemicals (should be absent)
 - (3) Geographic extent of project
 - (4) Dune sedimentology
 - (a) Degree of compaction retained (should be high)
 - (b) Sediment penetrability (should be maintained)
 - (c) Vegetation (should be restored)
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dunes on the high beach. Densities of *Emerita talpoida* were reduced by 35–37%, whereas *Donax* spp. densities were generally higher on bulldozed beaches. The impact on prey for surf fishes is therefore probably minimal because (1) ghost crabs are not a part of any fish diet and (2) the two taxa that are important prey for surf fishes, *Emerita* and *Donax*, exhibited approximately equal but opposite and compensatory effects. This study, like most earlier ones, did not last long enough to document complete recovery from the disturbances and did not evaluate the impacts of turbidity.

Beach-nourishment projects include several controllable variables that both a review of the assessment studies (Nelson, 1989, 1993) and a basic first-principles understanding of the ecology of the invertebrates of soft sediments (Brown and McLachlan, 1990) suggest are important in determining the degree of surf-fish habitat degradation associated with such projects (Table 2). First, because the mole crabs and bivalves occupy the intertidal beach only during the warmer months and spend the remainder of the year subtidally (Leber, 1982), the seasonal timing of nourishment activities can greatly influence the numbers of invertebrates killed. Furthermore, if the sediments are added to the intertidal beach early enough to be acted upon by physical transport processes for some time before the spring-summer seasons of larval settlement, then acceptable sediment conditions may be more likely to return in time to offer larvae an attractive habitat for metamorphosis and colonization. Second, the character of the sediments is critical. It involves at least four aspects: sediment grain size, abundance of mud balls, concentration of shell debris, and chemical toxicity. Grain size is a major determinant of species composition in soft sediments, and *Emerita* is known to be sensitive to it (Bowman and Dolan, 1985). The mud balls represent a continuing source of local turbidity long after cessation of the nourishment activity. Similarly, any silts and clays in the deposited sediments can be eroded and resuspended, elevating turbidity levels for many months. Shell debris affects burrowing capability of the benthic invertebrates of the intertidal beach (L. Manning, unpubl. data) and may lead to lower densities as waves transport the slow burrowers off the beach and along shore. If sediments for nourishment are obtained from depositional sites, especially if the source is a commercial harbor, the fine sediments can be contaminated by heavy metals or synthetic organic compounds that may be toxic to settling larvae or later life stages of the beach invertebrates. Third, the linear extent of the nourishment project can affect the rate of recovery of the benthos because, if a long enough stretch of beach is

nourished, longshore transport and immigration of juvenile and adult animals cannot readily contribute to recovery.

The U.S. Army Corps of Engineers enforces some controls on the beach-nourishment process, and state resource agencies and commissions enact rules designed in part to protect the ecology of the beach system. For example, the U.S. Army Corps of Engineers requires mean grain size to exceed 0.07 mm in diameter so as not to differ too much from naturally coarse beach sand. The Coastal Resources Commission (CRC) in North Carolina restricts these beach-disturbing activities to the colder season, before the end of April. Nevertheless, it is obvious that these controls are inadequate to protect the essential surf fish habitat of the intertidal beach. The constraints on sand-grain size appear to be too liberal to be protective, and the season for beach disturbance is not sufficiently constrained to the months of little risk, either because the regulations are inadequately restrictive or because they are not followed faithfully, as variances are routinely granted. In southwest Florida, beach nourishment is typically carried out in summer so as to minimize interference with the winter tourism trade, but this decision maximizes damage to the habitat for pompano and other surf fishes. It is unclear whether the inclusion of mud balls and shell hash is problematic because properly designed assessment studies have not been conducted, despite the potential for regulating these activities in ways that do not degrade essential fish habitat yet still allow the projects to continue. Similarly, the time frames of assessment are typically far too short (only a few weeks or months following termination of the project) to allow confident predictions of complete recovery times. Principles of ecosystem management suggest that the agencies responsible for fragments of regulation and management should come together to produce a coordinated conservation plan. They must also institute appropriate adaptive management by conducting the studies necessary to determine how to minimize habitat damage resulting from beach nourishment, bulldozing, and other habitat-degrading measures taken in response to shoreline erosion.

SUBTIDAL OYSTER-REEF HABITAT

Subtidal oyster reefs and the oyster fishery that they support have both been in decline along the east coast of North America for nearly a century (MacKenzie, 1996). The decline has been especially dramatic over the past three decades. Fishery landings of eastern oysters harvested from wild stocks are down by at least one order of magnitude in most of the estuaries of the Atlantic coastal states. The areal cover of subtidal reef habitat has declined, for example in Chesapeake Bay by over 50% (Hargis and Haven, 1988; Rothschild et al., 1994), and the remaining reefs have been greatly reduced in stature (Marshall, 1954; DeAlteris, 1988). Native oysters are effectively extinct in many other regions worldwide, such as Europe and the west coast of North America. Several causes have been suggested for the decline in the eastern oyster, including prominently water-quality problems, diseases, habitat destruction, and overharvest (see, e.g., Seliger et al., 1985; Hargis and Haven, 1988; Rothschild et al., 1994; Ford and Trip, 1996; Hofmann and Powell, 1998). The existence of multiple causes for the oyster's demise has paralyzed management despite the realistic potential to restore both oyster reefs and the goods and services that they provide as habitat for oysters and several fin- and shellfishes (Lenihan and Peterson, 1998).

Subtidal oysters can be characterized as 'ecosystem engineers' (Jones et al., 1994), in that they create biogenic habitat with physical structure providing important resources for other species (Bahr and Lanier, 1981). They establish reefs of hard structure naturally rising meters in elevation (Marshall, 1954; DeAlteris, 1988) above an estuarine seafloor, which is otherwise relatively flat and composed of unconsolidated, mobile sediments. Oysters themselves recruit onto and grow on the shells of other oysters, thereby extending the reef upward over time. Many species of benthic invertebrates (Wells, 1961; Bahr and Lanier, 1981) and fishes (Arve, 1960; Lenihan et al., in press) occupy the engineered reef habitat. The oyster reef is the temperate-zone analog of the tropical coral reef, which likewise provides a complex, three-dimensional habitat of hard surface upon which numerous other species depend. The use, abuse, and overuse of oyster dredges has, in the process of extracting oysters, gradually mined and eroded the reefs, markedly reducing their height (Marshall, 1954; Hargis and Haven, 1988; Lenihan and Peterson, 1998).

A study by Lenihan and Peterson (1998) in the Neuse River estuary of North Carolina illustrates the fundamental way in which two factors affecting oyster survival, water quality and reduction in reef habitat stature, interact to dictate patterns of mortality of oysters. By contrasting present-day oyster reefs with historical information on elevations of those same reefs and by subjecting reefs to experimental oyster dredging, Lenihan and Peterson (1998) showed that fishing had probably reduced the elevations of oyster reefs in the Neuse River by at least a meter, as in Chesapeake Bay. They therefore used oyster shell to construct restored oyster reefs of two elevations, tall (2-m) reefs, corresponding more closely to natural, undegraded reef habitat, and short (1-m) reefs reflecting the present-day conditions. Replicate reefs of each elevation were constructed at each of three water depths, 2, 4, and 6 m. Oysters naturally colonized the shell matrix, which allowed an evaluation of how the contrasting physical, chemical, and sedimentological environments induced by reefs of different elevations affected oyster settlement, growth, and survival (Lenihan, 1999). Here we describe only the results for oyster survival and responses of reef-associated fishes and their crustacean prey during major events of oxygen depletion in the bottom waters of the estuary.

The primary production of microalgae in the Neuse River estuary is limited by nitrogen (Paerl et al., 1995), as is typical in estuarine waters. Microalgal productivity in this and other estuaries has been greatly increased by nutrient additions from increased fertilizer use, discharge of animal and human wastes, conversion and destruction of riparian wetlands, and increased atmospheric deposition (Paerl, 1985; Cooper and Brush, 1991; Nixon, 1995). This eutrophication of estuaries like the lower Neuse River has led to increased algal production, which intensifies biological oxygen demand as microbial decomposition of algae occurs after algal cells settle to the estuarine seafloor (Paerl et al., 1995, 1998). During periods of density stratification of the water column, caused by low wind stress and freshwater runoff overlying a wedge of saltier water at depth, severe hypoxia (dissolved oxygen $<2 \text{ mg L}^{-1}$) and anoxia can occur in the bottom waters of these systems. These oxygen-depletion events occur in summer and fall, when warm temperatures increase rates of microbial activity, when surface heating helps intensify stratification, and after earlier plankton blooms and/or land runoff have loaded the system with labile organic matter. Wind mixing is sufficient only to mix enough oxygen to supply surface waters: the density stratification prevents the oxygen from replenishing deeper waters. Consequently, when these hypoxia/anoxia events occur in estuarine systems, they are most intense and persistent as a layer of oxygen-depleted bottom water. Oysters are toler-

ant of short periods of low dissolved oxygen, but exposure to severe hypoxia or anoxia for multiple days can result in mass mortality of both oysters and relatively sedentary reef-associated organisms (Seliger et al., 1985; Breitburg, 1992).

By placing tall and short restored oyster reefs in both shallow and deep water, Lenihan and Peterson (1998) indirectly manipulated both the degree of exposure to hypoxia/anoxia and the habitat degradation induced by dredge fishing. By censusing oysters before and after a 16-d period of bottom water hypoxia/anoxia in summer 1994, Lenihan and Peterson (1998) showed that all oysters more than 5 m below the water surface were killed, whereas survival on all reef surfaces less than 5 m below the surface was virtually 100%. This result reveals that one of the functions of an oyster reef is to elevate the oysters and associated organisms into the upper water column, that is, into a refuge against exposure to bottom water hypoxia/anoxia (Seliger et al., 1985; Breitburg, 1992). Inadequate protection of oyster-reef habitat from mining by dredges during harvest has resulted in great reduction in the height of the reefs and therefore increased exposure of the entire reef system to much higher risk of mortality from low-oxygen stress. In addition, relatively sedentary crustaceans associated with reefs—amphipods, shrimps, and small crabs—showed mass mortality during a similar 19-d hypoxic/anoxic event in summer 1997 (Lenihan et al., in press). Burrows occupied by blue crabs just before the oxygen depletion event were uniformly abandoned below 5 m (Lenihan and Peterson, 1998). A group of 18 species of large, mobile fishes, all of which have commercial and/or recreational value, abandoned the short reefs in deep water and the bottoms of tall reefs in deep water during the 1997 hypoxic/anoxic event and were displaced to reefs in shallow water (Lenihan et al., in press). One consequence of this concentration of demersal reef-associated fishes on reefs in shallow water was a decrease in densities of their crustacean prey by over 50% during the event (Lenihan et al., in press). Even during periods free of oxygen stress, tall reefs function to provide a physical and chemical environment of faster current flows that enhances the growth and physiological condition of oysters, rendering them more resistant to infection by the oyster disease ‘dermo’ and reducing the disease’s effects on those that do contract it (Lenihan et al., 1999). Thus reef height, one measure of habitat quality, also interacts with a major oyster disease.

Although periods of benthic oxygen depletion in mesohaline regions of estuaries occur naturally (Stanley and Nixon, 1992), human activities have greatly increased their frequency, intensity, and extent (Cooper and Brush, 1991; Turner and Rabalais, 1994; Paerl et al., 1995, 1998). More restrictive controls on nutrient loading—such as lower mass limits on point-source discharges, stormwater controls, buffer requirements, water management structures, and effective regulation of agriculture to reduce nonpoint-source loading—should reduce the impact of oxygen depletion on oyster-reef habitat but cannot solve the whole problem without fisheries management designed to prevent removal of the tops of reefs by dredges, where refuges from oxygen depletion can exist. Only integrated management by the scattered agencies responsible for water quality, land use, and fisheries can solve these problems.

ESTUARINE SOFT-SEDIMENT HABITAT

A large fraction of the total commercial and recreational landings of the southeastern United States is derived from demersal species with juvenile nurseries in estuarine soft-

bottom habitat. These demersal crab, shrimp, and fish stocks represent the majority of dollar value of commercial harvests: in North Carolina, for example, nine species dependent on estuarine soft-bottom habitat accounted for \$226 million in dockside value between 1994 and 1996, compared to \$103 million for all other commercial fishery landings combined (data from the North Carolina Division of Marine Fisheries). Blue crabs feed on benthic bivalve molluscs that have thin shells, like *Macoma*, and do not burrow deeply, such as juvenile *Mya* (Blundon and Kennedy, 1982; Eggleston et al., 1992; Ebersole and Kennedy, 1995), as well as other relatively large benthic invertebrates and scavenged fishes (Hines et al., 1990). Brown shrimp consume benthic meiofauna and small macrofaunal invertebrates as well as detrital materials (Bell and Coull, 1978; Hunter and Feller, 1987; McTigue and Zimmerman, 1998). The diets of some juvenile sciaenids, such as spot, are dominated by clam siphons during late spring and early summer, then broaden to whole clams and other larger soft-bottom invertebrates later (Hodson et al., 1981; Sutherland, 1982; Peterson and Skilleter, 1994). Other species in the drum family and juvenile flounders also prey predominantly on relatively large soft-bottom invertebrates during their nursery phase in the estuary.

In mesohaline regions of estuaries, the availability of soft-sediment prey resources for these demersal fish and shellfish using the system as a juvenile nursery or feeding grounds can be reasonably expected to vary in response to the history of disturbance to the benthic system. The disturbance of most wide-ranging and intensive impact on the benthos in these regions of the estuary is the warm-season hypoxia/anoxia discussed above. The entire fauna of the soft-sediment seafloor is killed by sufficiently long exposure to anoxia (Tenore, 1972; Santos and Simon, 1980b; Diaz and Rosenberg, 1995). With the return of oxygen, the benthic invertebrate community can initiate a process of successional recovery (Santos and Simon, 1980b; Hall, 1994). It is reasonable to presume that the value of the benthos as feeding habitat for demersal fishes is negligible during a hypoxic/anoxic event because the fish emigrate from the oxygen-depleted waters. Immediately after anoxic events, moribund benthic invertebrates may feed returning demersal fishes (e.g., Pihl et al., 1992), but hypoxia intense enough to strip the seafloor of life would shortly reduce the value of the benthic habitat for demersal fishes to near zero. Recovery of habitat value then depends on how abundant key prey resources become during the sequential stages of community succession in the benthos (Diaz and Rosenberg, 1995). Because fishes and shellfishes can differ radically in the prey types used, these various consumers may be best served at different stages of succession of the benthic community (Pihl, 1994; Thomson, 1998).

The pattern of invertebrate succession in uninhabited soft sediments has been frequently described empirically in the literature. Conceptual models of the successional process were initially driven by a desire to predict biological recovery after deposition of dredge spoils (McCall, 1977; Rhoads et al., 1978). These models predict succession as a joint function of the changing geochemistry of the sediments and the life history differences among benthic animals. Such considerations should be the critical determinants of successional recovery after any major disturbance of soft sediments (Hall, 1994). The Rhoads et al. (1978) model predicts that faunal succession will proceed by initial colonization of sediments by surface-dwelling and shallow-burrowing animals, which can avoid the toxic sulfides in the anoxic layers of the sediments rising close to the sediment surface. As succession progresses, the bioturbation of the surface sediments by mobile invertebrates will mix oxygen to increasing depths in the sediments and allow occupation by succes-

sively larger, more deeply burrowing benthic animals. As in any successional sequence, the life histories of component species are expected to change during succession; short-lived opportunists will arrive and dominate early, and longer-lived 'climax' species will succeed them through time (Grassle and Grassle, 1974; McCall, 1977). The mobility of many juvenile and adult invertebrates complicates this life history prediction somewhat because of the potential for colonization to proceed partly by larval settlement and partly by immigration (Santos and Simon, 1980a; Thrush et al., 1996). Nevertheless, by combining knowledge of diets of demersal consumers and likely sequences of succession in the benthos, one could reasonably hypothesize that demersal species like shrimp that prefer small surface invertebrates and detrital materials would be better served by early successional stages and that demersal species like juvenile sciaenids would be better served by later successional stages when adult bivalves with longer siphons and larger polychaetes and other invertebrates would dominate the benthos. Blue crabs may also be favored by somewhat earlier successional stages, when bivalves have not yet developed thick shells and the size to burrow deeply (Zwarts and Wanink, 1989). This hypothesis could explain why shrimp fisheries appear to be so sustainable despite the repeated and extensive disturbance of the bottom habitat by trawls used in the fishery (Northridge, 1991; Van Dolah et al., 1991; Dayton et al., 1995).

The hypothesis that the habitat value of the soft-bottom benthic estuarine community depends on successional stage and varies with type and species of demersal fish and shellfish has been tested only in one area, the Kattegat (Pihl, 1994), so the generality of patterns cannot yet be established. Such generalization is critical to protection of essential fish habitat. By sampling the benthic invertebrate community on multiple cross-river transects covering the lower Neuse River estuary in June before and in late August after the season of hypoxic/anoxic events, Thomson (1998) tested one component of this hypothesis. She showed that benthic community composition and abundance of *Macoma balthica* were uniform across depth on any given transect in June but changed by August at all sites where hydrographic information indicated extended exposure to severe hypoxia/anoxia. *M. balthica* density declined to zero where exposed to oxygen deprivation and remained at higher levels elsewhere. Benthic community composition was also uniform across river before exposure to severe hypoxia/anoxia at depth in summer, but after exposure the exposed stations segregated out strongly in ordination analyses. The implications of such effects of water quality on habitat value for various types of demersal fishes have yet to be explored, but severe hypoxia/anoxia clearly resets the benthic community to an earlier successional stage, in the pattern generally expected from the Rhoads et al. (1978) model. Because this earlier successional stage lacks *M. balthica* and other large bivalves, whose siphons feed juvenile sciaenids, and lacks larger polychaetes that also serve as prey for these fishes, the productivity of sciaenids is probably greatly reduced by hypoxia/anoxia. In contrast, the value of the benthic community may be increased for brown shrimp, if the smaller meiofaunal and other benthic prey are more abundant in earlier stages of succession. The increasing eutrophication of coastal estuaries from a wide variety of sources implies higher frequencies, greater spatial extents, and longer durations of anoxic events, with associated implications for alteration of the suitability of the soft-bottom habitat for producing fish and shellfish. Because the consequences of eutrophication for essential fish habitat have not been directly demonstrated, incentive for reducing the nutrient loading that is its cause is weak. Reduction of nitrogen from point-source discharges (such as municipal and industrial waste-treatment plants)

and from nonpoint sources (such as concentrated animal feedlot production, stormwater runoff, and atmospheric releases from automobiles and industrial smokestacks) may be required to protect estuarine soft-bottom habitat and sustain production of estuarine-dependent fisheries.

DISCUSSION

The three essential fish habitats discussed here, which currently lack protection sufficient to ensure sustained fish production, all share two broad characteristics. First, appreciation of the current and future threats to each of these three habitats—the high-energy ocean beach, subtidal oyster reef, and estuarine soft bottom—requires an integration of disciplines, benthic ecology and fisheries oceanography with fisheries management. Second, solving the problems that endanger them requires management actions that cut across traditional management jurisdictions: the present fragmented scheme of management is inadequate to protect essential fish habitat. The solution to better appreciation of such threats and to protecting against them lies in adopting a more holistic approach, as argued by proponents of ecosystem management (Christensen et al., 1996; Botsford et al., 1997; Fogarty and Murawski, 1998).

Before the pioneering work of Hjort, Ricker, and Beverton, which established the new discipline of quantitative fisheries biology, fisheries science and ecology were treated as a single discipline. After decades of separation, ecology and fisheries biology have again been drawn together into a field broadly defined as fisheries oceanography (see, e.g., Sinclair, 1988; Cushing, 1995). This represents a critical step forward in forging the interdisciplinary linkages necessary to evaluate important problems in fisheries management, such as exploring how the physics and biology of the ocean interact to cause critical temporal and spatial variation in fish recruitment. This recombination of disciplines must now proceed a step further: to address the pressing problems in protection of habitat for demersal fishes, it must effectively merge the fields of benthic ecology and fisheries science. The earliest research in benthic ecology, done in Scandinavia, was driven by questions of the relationships of benthos to fish feeding (e.g., Blegvad, 1928), and recent work has continued to find some relationships between fishes and benthic communities, so merger of these fields would be another example of returning to the more holistic approaches of the past. Several modern benthic ecologists have worked in this interface between benthic community ecology and fish habitat function (e.g., Arntz, 1979; Summerson and Peterson, 1984; Eggleston, 1990; Dayton et al., 1995; Crowder et al., 1997), but much more emphasis on this partnership is required to determine the nature of the threats to essential habitat for demersal fishes. A missing element until recently has been understanding of fish behavioral reactions to habitat variables. Analysis and modeling of individual behavior of fish is critical to creating more holistic landscape-scale protection of habitat function (e.g., Irlandi and Crawford, 1997). For example, Micheli and Peterson (1999) combined methods of benthic community ecology and consumer behavioral response to habitat to show that vegetated corridors induce blue crabs to move more freely among habitat patches, probably by allowing them to avoid risk of avian predation (Micheli, 1997).

Although the Magnuson-Stevens Fisheries Conservation and Management Act is federal legislation and NOAA's National Marine Fishery Service has active programs to pro-

Table 3. Management authorities sharing responsibility for estuarine water quality that affects oyster-reef habitat and soft-bottom habitat in North Carolina (used as an example) and the variables they control.

N.C. Marine Fisheries Commission	bottom disturbance from fishing gear
N.C. Environmental Management Commission	stormwater runoff, atmospheric N emissions, point-source discharges of nutrients and BOD, runoff from concentrated animal feedlot operations, groundwater quality
N.C. Sedimentation Control Commission	erosion of soils into rivers
N.C. Coastal Resources Commission	integrity of waterfront wetland buffers in 20 coastal counties
N.C. Soil and Water Division	farming practices
U.S. Environmental Protection Agency	Clean Water Act provisions for antidegradation, Clean Air Act provision for acid rain controls

tect and restore the function of many fish habitats (e.g., Thayer, 1992), the major present and future threats to the habitats described here come from human activities regulated by state agencies. In each case, multiple state agencies are involved because each has responsibility for a different aspect of the environment. The surf fish habitat of the high-energy sand beach, for example, is degraded by beach nourishment jointly regulated by the federal Army Corps of Engineers and state coastal-resource agencies (the Coastal Resources Commission in North Carolina). Yet, protection of surf fish habitat should be a responsibility of state fisheries-management agencies as well. The present lack of coordinated management clearly sacrifices conservation of surf-fish habitat for the protection of shoreline development against erosion, when both goals could be simultaneously achieved by integrated management across multiple state and federal authorities. Requirements to match sand characteristics more closely to natural beach sand and enforcement of policies that restrict nourishment to biologically inactive seasons could allow nourishment to continue without the degree of beach habitat degradation currently permitted.

Degradation of oyster-reef habitat results from joint management inaction by state water-quality authorities and state fisheries-management agencies (Table 3). Controls on nutrient loading into estuaries even involve authorities charged with regulating air emissions of nitrogen oxides and with overseeing farming practices that release atmospheric ammonia (Paerl et al., 1998). The physical integrity of the oyster reef is the responsibility of state fisheries agencies, whose present regulations allow habitat degradation by permitting use of habitat-damaging dredges. Alternative methods exist, notably hand harvest by divers, that could reduce or even eliminate habitat damage from oyster fishing while retaining present efficiency of harvest (H. S. Lenihan, unpubl. data), but present management practices have failed to take the bold steps required to protect and restore oyster-reef habitat. Panels established expressly to address the problem of declining oyster fisheries

in Maryland, Virginia, and North Carolina have made explicit recommendations for restoring and protecting the oyster-reef habitat, including experimental establishment of oyster-reef reserves, that have gone largely unheeded (e.g., Frankenberg, 1995). Again, the institutional structures for achieving the holistic management required for protection of essential fish habitat in areas under state jurisdiction are fragmented, unwieldy, and ineffective in dealing with problems requiring holistic environmental approaches. Perhaps oyster reefs should be considered habitat and authority for their protection granted in part to the NOAA habitat division, rather than remaining with the state fisheries agencies, which continue to allow destructive fishing practices.

Degradation of the soft-bottom habitat for estuarine demersal fish and shellfish by growing cultural eutrophication involves the same set of state management authorities as the oyster-reef example (Table 3). These include agencies responsible for managing air emissions, agricultural emissions and runoff, and surface water quality. Essentially, the entire spectrum of terrestrial land uses has implications for nitrogen loading of estuaries and coastal oceans (Paerl et al., 1998). The implications of eutrophication for fish habitat degradation and fish production are not yet well documented scientifically, but enough is known to support aggressive actions to reduce nitrogen loading of estuarine systems. Although we have addressed effects of eutrophication on habitat for demersal fishes, water-column fishes experience analogous problems during hypoxic/anoxic events: fish kills are induced, and the unnaturally high densities of fishes in small refuges of oxygenated waters near shore can reduce survival through intense predation and competition (L. Eby and L. Crowder, unpubl. data). Unfortunately, the institutional complex of contributing management authorities represents a barrier to efficient, effective, and coordinated action. The federal EPA is becoming more demanding in its interpretation and enforcement of the federal Clean Water Act by requiring state water-quality agencies to impose TMDLs (total maximum daily loads) in management plans for river basins. In addition, more rules on previously unregulated agricultural practices involving nutrient loading from concentrated animal-production facilities may help address a component of the eutrophication problem. Here too, however, holistic management in the spirit of ecosystem management is required, as exemplified by the program established for the Chesapeake Bay. Management of essential fish habitats in estuaries will require integration into basinwide models and plans for water-quality maintenance, which themselves must include airshed inputs of nutrient deposition.

The three fish habitats described above illustrate the failure of present management of essential fish habitat. The failure can be traced both to inadequate scientific research addressing the technical problems and to fragmentation of the institutional structures for management of fish habitat. Serious response to the new mandates for protection of essential fish habitat will require new dedication to more holistic research in the arena of environmental problem solving (Peterson, 1993). More challenging by a good measure will be the need to merge now-separate management authorities to create a form of ecosystem-based management to forge effective solutions.

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