

The Role of Oyster Reefs as Essential Fish Habitat: A Review of Current Knowledge and Some New Perspectives

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Abstract.—The importance of molluscan-dominated systems (e.g., oyster reefs, mussel beds, vermetid gastropods) to the maintenance of commercially and ecologically important species has not been as broadly recognized as has been the importance of other structurally complex estuarine habitats such as sea grass beds and salt marshes. As a consequence, these systems have often been unappreciated and understudied. Important ecosystem services of molluscan-dominated systems include: (1) filtering capacity; (2) benthic–pelagic coupling; (3) creation of refugia from predation; (4) creation of feeding habitat for juvenile and adult mobile species as well as sessile stages of species that attach directly to molluscan shells; and (5) provision of nesting habitat. Destructive harvesting and overfishing can reduce habitat extent and impair habitat functioning. Only recently have ecosystem services been incorporated into the management of these systems. The role of oyster reefs as “essential fish habitat” falls into two principal categories: (1) reefs as habitat for oysters and (2) reefs as habitat for resident and transient species. Although the former role has received some attention as part of efforts to restore oyster resources, the latter role remains largely unexplored. The role of oyster reefs as critical habitat for other species is suggested by the diverse fauna associated with them; however, the factors that control the development of these reef-associated assemblages are generally unknown, and enumeration of specific habitat services using replicated field experiments is just beginning. Using data summarized from studies in Maryland, Virginia, North Carolina, South Carolina, and Texas, we classify finfish assemblages associated with reefs based upon the degree of their association and include an extensive finfish and decapod species list. We conclude, within the context of the current state of knowledge, that (1) the construction of reef bases using materials that provide adequate vertical relief and interstitial space and (2) the establishment of broodstock sanctuaries protected from harvesting pressure are important for restoring oyster populations. Utilization of reef habitats by numerous commercially, recreationally, and ecologically important species across a wide geographic range likely portends the reef habitats’ importance as essential fish habitat, but many functional relationships remain to be evaluated. Future oyster habitat research needs include (1) defining the morphological and spatial reef characteristics that support enhanced oyster growth and survival; (2) improving understanding of how harvest methods affect reef integrity and function; (3) determining the critical services provided by reef habitats in the life cycles of important species; and (4) further clarifying the trophic links between the resident fauna on oyster reefs and transient species.

Approximately 75% of the commercial fish and shellfish species of the United States depend on estuaries at some stage in their life cycles (Chambers 1992), and the continued health and productivity of these finfish, mollusc, and crustacean populations are in large part dependent on the quantity and quality of appropriate nursery and adult habitats (e.g., Heck and Wetstone 1977; Heck and Orth 1980; Nixon 1980; Boesch and Turner 1984; Heck and Thoman 1984; Orth et al. 1984; Orth and Van

Montfrans 1987; Zimmerman et al. 1989; Wilson et al. 1990; Barshaw et al. 1994; Haywood et al. 1995; Peterson and Lubchenco 1997). Plants such as submerged aquatic vegetation (SAV) or emergent vegetation (marshes and mangroves) typically dominate critical habitats within estuaries. The 1996 reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act (Public Law 104–208) included an explicit goal to protect, restore, and enhance all “essential fish habitats” (henceforth referred

to as EFH). The law defined EFH as “those waters and substrate necessary to fish for spawning, breeding, feeding, and or growth to maturity,” and “fish” was defined to include “finfish, molluscs, crustaceans, and all other forms of marine animal and plant life other than marine mammals and birds” (USDOC 1997). The ability of fishery managers to identify EFH depends on the availability of information on various habitats. For many habitats, a wealth of information is available, but for other habitats information is scarce. Therefore, as part of the habitat information-gathering process, it is important to understand the extent to which estuaries and specific estuarine habitats serve as EFH and what estuarine habitat characteristics are most important to EFH-related processes.

There is no question that oyster reefs qualify as EFH because of the importance of reefs to the oysters themselves. However, we are just beginning to understand what precise characteristics of oyster reefs enhance oyster recruitment, growth, and survival. In addition, recent research has highlighted the importance of oyster reefs to ecosystem-level processes and as habitat for fishes and macroinvertebrates other than oysters. In this paper we summarize the current state of our knowledge of oyster (specifically the eastern oyster *Crassostrea virginica*) reefs as (1) important to ecosystem-level processes in estuaries; (2) essential habitat for oysters; and (3) important habitat for ecologically, commercially, and recreationally important finfish and crustacean species. We include in this study existing descriptive data on oyster-reef habitat ecology and recent and ongoing experimental investigations that are relevant to understanding how the structure and ecological function of oyster reefs may be incorporated into an EFH framework. We also discuss issues relating to tradeoffs between habitat and resource management and protection, the value of areas closed to harvesting due to poor water quality, and habitat restoration and enhancement (see Coen and Luckenbach, in press, for more information on habitat enhancement).

Decline of the Oyster Fishery and Reef Habitat

The range of the eastern oyster *Crassostrea virginica* (Gmelin) extends from the Saint Lawrence River in Canada to the Atlantic coast of Argentina (Carriker and Gaffney 1996), with introductions into the northwest Pacific region of the United States.

The eastern oyster is a reef-forming organism, but it varies throughout its range in habitat and growth form. Eastern oyster reefs may be intertidal or subtidal, fringing or patch reefs, and may vary in size from a few square meters to many hectares. Greatest abundances are found in areas where a partial predation refuge exists, such as low-salinity (<15 ppt) waters or in the intertidal zone (e.g., MacKenzie 1983, 1996a, 1996b; Burrell 1986; Kennedy et al. 1996).

Although intensive, hatchery-based aquaculture of oysters is increasing in the United States, the oyster fishery historically has been based upon wild stocks. Some areas in the United States still have wild oyster stocks supporting valuable fisheries (see MacKenzie et al. 1997a, 1997b), but most stocks are in decline owing to the following factors (Gross and Smyth 1946; MacKenzie 1983, 1996a, 1996b; Rothschild et al. 1994; Kennedy et al. 1996; NOAA 1997; Lenihan and Peterson 1998; Hargis and Haven, in press; Luckenbach et al., in press):

- overfishing and associated habitat destruction;
- shortages of oyster cultch (i.e., shell or other hard substrate);
- disturbance (e.g., dredging, boating, storms);
- reduced water and habitat quality;
- alteration of natural flow and salinity patterns;
- natural and introduced predators and competitors; and
- oyster disease pressures.

Between 1880 and 1910, the oyster fishery peaked at more than 72.7 million kg of meat per year (Brooks 1891; MacKenzie 1996a), but by 1995, U.S. landings had declined to 18.4 million kg (MacKenzie 1996a). The once highly productive fisheries of the Chesapeake and Delaware Bays and North Carolina (Frankenberg 1995) have virtually collapsed. Although diseases are often cited as the reason for recent declines, overharvesting and resultant habitat destruction with little shell replacement (considered analogous to strip mining by some [see Hargis and Haven, in press]) have certainly been major causes for the dramatic declines throughout much of the mid-Atlantic region (see Brooks 1891; Gross and Smyth 1946; Rothschild et al. 1994; Lenihan and Peterson 1998; H. Lenihan and F. Micheli, University of North Carolina, unpublished data).

Oyster fishing methodologies, such as hand- and hydraulically operated tongs, dredges pulled by sailing and motor-powered vessels, and hand-harvest-

ing on intertidal reefs, have been particularly destructive to the reef matrix (reviewed in Hargis and Haven 1995, in press; MacKenzie 1996a; MacKenzie et al. 1997a, 1997b; Lenihan and Peterson 1998; Lenihan and Micheli, unpublished data). In addition, size restrictions placed by fisheries managers as well as market demand may result in small oysters being culled from the catch and returned to the water. In these situations, the oysters are no longer attached to the reef, and the damage to the reef may be significant (see Burrell et al. 1991; L. Coen, South Carolina Department of Natural Resources, personal observations; Lenihan and Micheli, unpublished data). Relaying—the practice of moving attached juvenile oysters on shell (also called “cultch”) to other areas—is commonly utilized to reduce mortality due to disease or to achieve better growth, but little information is available on the relative survival of these “redeployed” oysters for different system configurations around the United States. For example, Klemanowicz (1985) and Burrell et al. (1991) evaluated impacts of relaying intertidal oysters and found significant impacts on survival that were strongly influenced by when harvesting occurred.

Two oyster protozoan parasites *Perkinsus marinus* and *Haplosporidium nelsoni* are now endemic in *C. virginica* throughout much of its range, causing epizootics in many but not all areas (Ford and Tripp 1996; but see Bobo et al. 1997). Specifically, *P. marinus*, the causative agent of “Dermo,” can be found from Maine to Mexico, and *H. nelsoni*, the cause of “MSX,” infects oysters from Maine to the Atlantic coast of Florida (Ewart and Ford 1993; Ford and Tripp 1996). Both diseases cause significant mortality, especially in oysters greater than two years of age, and often have been given too much credit as the primary cause of the collapse of the northeastern oyster fisheries (see Rothschild et al. 1994; Paynter foreword in Brooks 1891, 1996 revised edition).

Efforts to sustain and enhance oyster fisheries have included (e.g., MacKenzie 1983, 1996a, 1996b; Leonard 1993; Kennedy et al. 1996; Andrews et al. 1997; Powell et al. 1997; Lenihan and Peterson 1998; Hayward et al. in press; Luckenbach et al., in press):

- developing broodstock sanctuaries;
- supplementing hard substrate with either natural or alternative materials (or cultch);
- relaying (defined above) seed and adult broodstock;

- improving water quality; and
- attempting in a limited manner to supplement natural populations with hatchery-reared stocks.

For example, Connecticut’s Long Island Sound oyster industry has recently seen a resurgence in landings from only 33,000 bushels in 1972 to a peak of nearly 900,000 bushels in 1992. Here resource restoration was successful due to improved water quality and unusual industry circumstances, including extensive bottom leases by a single major company and intensive bed manipulations (MacKenzie et al. 1997a; Goddard 1998; J. Volk, Connecticut Department of Agriculture, personal communication). However, in 1998, both Dermo and MSX, previously rare in Long Island Sound, significantly impacted these beds.

Oyster Reefs as EFH for Oysters: Critical Characteristics

Reef environments have generally been recognized as essential for oysters for aggregation of spawning stock, chemical induction of gregarious settlement, and predator refugia. Reef environments also provide oysters with a means of coping with siltation. Re-shelling programs conducted by most oyster-producing states point to the critical importance of reef habitat in supporting oyster population growth. Recent research has highlighted the contribution of particular reef characteristics to the recruitment, growth, and survival of oysters, and thus the EFH value of reefs to the oysters themselves. Among these characteristics are reef height (Lenihan and Peterson 1998) and the quality and quantity of interstitial spaces for recruiting oysters (Bartol and Mann, in press). Lenihan (1996), Lenihan and Peterson (1998), and Lenihan et al. (in press) constructed experimental subtidal reefs varying in morphology, water depth, and location within North Carolina’s Pamlico River estuary. To date these studies have demonstrated that subtidal oyster growth, survival (Lenihan and Peterson 1998), and disease dynamics (Lenihan et al., in press) vary with position on reefs in relation to flow velocity, sedimentation rate, and dissolved oxygen regimes. In addition, these studies, especially for stratified estuaries, indicate that placement of materials for subtidal reef habitats requires prior knowledge of local hydrographic conditions (i.e., current velocities, sedimentation rates, temperature and density stratification, and oxygen levels).

Bartol and Mann (in press) have reported the importance of interstitial space within a reef for oyster recruitment and survival. On a large, constructed intertidal reef with a small tidal amplitude in the Piankatank River, Virginia, Bartol and Mann observed that survival of oysters was greater below the reef surface, in the interstices between shells, than on the reef surface itself. Interstitial spaces presumably provide settlement sites with adequate water flow for spat growth and survival while providing a partial refuge from predation. These findings have implications for the types of substrates and planting configurations needed to support the development of oyster populations and epifaunal assemblages on constructed reefs.

Ecosystem Services of Oyster Reefs

Molluscan-dominated assemblages (e.g., oyster and vermetid gastropod reefs, mussel beds, and clam beds) can have significant impacts on population, community, and landscape-level processes (e.g., Cloern 1982; Safriel and Ben-Eliahu 1991; Paine 1994; Dame 1996). The importance of these assemblages stems both from their ability to filter large quantities of water (e.g., Newell 1988; Dame 1996) and the fact that some of these molluscs (including oysters) generate the primary structural habitat where they are common and thus act as ecosystem engineers (*sensu* Jones et al. 1994; Lenihan and Peterson 1998). In addition, much of our knowledge of marine communities derives from research on rocky shores, and these communities often are dominated by mussels (e.g., reviewed in Paine 1994; see also Petraitis 1987, 1995; Witman 1987).

There is good evidence that large numbers of suspension-feeding bivalves (or their absence) can have a significant impact on basinwide ecosystem attributes (Cloern 1982; Cohen et al. 1984; Dame 1996). Numerous studies point to the vast filtration capacity of dense bivalve populations as contributing to the control of water column phytoplankton dynamics. Specifically, these studies have focused on:

- clams in San Francisco Bay (Cloern 1982);
- cockles and mussels in the Oosterchelde estuary, Netherlands (Smaal and Haas 1997);
- asiatic clams in the Potomac River, United States (Cohen et al. 1984);
- zebra mussels in the Hudson River, United States (Roditi et al. 1996); and

- oysters in tidal creeks, South Carolina (Dame et al. 1992).

For example, intertidal oysters in South Carolina alter phytoplankton concentrations and energy flow rates in overlying waters (Dame et al. 1984, 1992; recently reviewed by Dame 1996). Similarly, Newell (1988) calculated that, before 1870, the Chesapeake Bay's oysters could filter the entire volume of the bay in 3.3 d. In contrast, the estimate for the same activity by reduced oyster populations in 1988 was 325 d. Recent ecosystem mass-action models have indicated that a return of significant oyster biomass could greatly decrease planktonic primary productivity and secondary gelatinous consumers to historically low levels and increase benthic primary and secondary productivity, thus potentially reducing Chesapeake Bay eutrophication (e.g., Ulanowicz and Tuttle 1992 and references therein). (See also Dame 1996 for a review of shellfish impacts on materials fluxes.)

Are Oyster Reefs EFH for Finfish and Other Macroinvertebrates?

Descriptive studies and reviews indicate that oyster reef communities along the Atlantic and Gulf coasts are highly diverse and include numerous species rare or absent in adjacent soft-bottom habitats (e.g., Wells 1961; Dame 1979; Bahr and Lanier 1981; Klemanowicz 1985; Burrell 1986; Stanley and Sellers 1986; Zimmerman et al. 1989). However, research including experimental manipulations is required to determine relationships among the different ecological functions of reefs (e.g., materials fluxes, provision of habitat, and trophic dynamics); the structural characteristics of reefs (e.g., oyster density, spatial extent, elevation, construction material); and the use and importance of oyster reefs to finfish and macroinvertebrate species other than oysters. Because of their large spatial scale, manipulations created by management and restoration activities will be an important tool in attempts to determine the importance of oyster reefs to species other than oysters (see recent reviews by Coen and Luckenbach, in press; Luckenbach et al., in press).

Finfish associated with oyster reefs can be divided into three categories: (1) reef residents, which use oyster reefs as their primary habitat; (2) facultative residents, which are generally associated with structured habitats and utilize oyster reefs as well as other habitat with vertical relief or shelter sites (e.g.,

TABLE 1.—Fishes and decapod crustaceans found on oyster reefs or in waters directly overlying reefs at Flag Pond (MD1; Breitburg, in press, unpublished data); the Patuxent River (MD2; D. Breitburg, the Academy of Natural Sciences, and T. Miller, University of Maryland, unpublished data); Piankatank River (VA1; J. Harding, Virginia Institute of Marine Science, unpublished data); Fisherman's Island (VA2; M. Luckenbach and J. Nestlerode, Virginia Institute of Marine Science, unpublished data); Neuse River and Pamlico Sound (NC; Lenihan et al. 1998); Inlet Creek and Toler's Cove (SC; Wenner et al. 1996; Coen et al. 1997, 1998; Coen and Luckenbach 1998, unpublished data) and West Bay (TX; Zimmerman et al. 1989).

Common name (scientific name)	MD1 ^a	MD2	VA1 ^b	VA2 ^c	NC	SC ^d	TX ^e
Oyster reef resident fishes							
gulf toadfish (<i>Opsanus beta</i>)							X
oyster toadfish (<i>Opsanus tau</i>)	X	X	X	X	X	X	
skilletfish (<i>Gobiesox strumosus</i>)	X	X	X	X	X		X
striped blenny (<i>Chasmodes bosquianus</i>)	X	X	X	X	X	X	X
feather blenny (<i>Hypsoblennius hentz</i>)	X	X		X	X		
freckled blenny (<i>Hypsoblennius ionthas</i>)							X
naked goby (<i>Gobiosoma bosc</i>)	X	X	X	X	X	X	X
Facultative resident fishes							
northern pipefish (<i>Syngnathus fuscus</i>)	X			X		X	
black sea bass (<i>Centropristis striata</i>)	X		X	X	X		
Atlantic spadefish (<i>Chaetodipterus faber</i>)	X		X		X		
darter goby (<i>Gobionellus boleosoma</i>)						X	
seaboard goby (<i>Gobiosoma ginsburgi</i>)				X			
Transient fishes							
Atlantic stingray (<i>Dasyatis sabina</i>)						X	
cownose ray (<i>Rhinoptera bonasus</i>)	X		X		X		
American eel (<i>Anguilla rostrata</i>)	X	X	X		X		
speckled worm eel (<i>Myrophis punctatus</i>)						X	X
glass eel (<i>Conger oceanicus</i>)				X			
blueback herring (<i>Alosa aestivalis</i>)			X				
gulf menhaden (<i>Brevoortia patronus</i>)							X
Atlantic menhaden (<i>Brevoortia tyrannus</i>)		X	X		X	X	
Atlantic herring (<i>Clupea harengus</i>)				X			
bay anchovy (<i>Anchoa mitchilli</i>)			X	X		X	X
striped anchovy (<i>Anchoa hepsetus</i>)				X		X	
carp (<i>Cyprinus carpio</i>)			X				
brown bullhead (<i>Ameiurus nebulosus</i>)		X					
channel catfish (<i>Ictalurus punctatus</i>)		X					
inshore lizardfish (<i>Synodus foetens</i>)	X				X		
spotted hake (<i>Urophycis regia</i>)			X				
sheepshead minnow (<i>Cyprinodon variegatus</i>)						X	
mummichog (<i>Fundulus heteroclitus</i>)				X		X	
rainwater killifish (<i>Lucania parva</i>)				X			
rough silverside (<i>Membras martinica</i>)				X			
inland silverside (<i>Menidia beryllina</i>)						X	X
Atlantic silverside (<i>Menidia menidia</i>)	X					X	
fourspine stickleback (<i>Apeltes quadracus</i>)				X			
lined seahorse (<i>Hippocampus erectus</i>)			X	X			
chain pipefish (<i>Syngnathus louisianae</i>)						X	
northern sea robin (<i>Prionotus carolinus</i>)			X	X			
bighead searobin (<i>Prionotus tribulus</i>)					X	X	X

Common name (scientific name)	MD1 ^a	MD2	VA1 ^b	VA2 ^c	NC	SC ^d	TX ^e
white perch (<i>Morone americana</i>)		X		X			
striped bass (<i>Morone saxatilis</i>)	X	X	X	X	X		
gag (<i>Mycteroptera microlepis</i>)				X	X		
green sunfish (<i>Lepomis cyanellus</i>)							X
bluefish (<i>Pomatomus saltatrix</i>)		X	X	X	X		
cobia (<i>Rachycentron canadum</i>)			X				
lookdown (<i>Selene vomer</i>)				X	X		
gray snapper (<i>Lutjanus griseus</i>)					X	X	
mahogany snapper (<i>Lutjanus mahogoni</i>)						X	
spotfin mojarra (<i>Eucinostomus argenteus</i>)				X		X	
pigfish (<i>Orthopristis chrysoptera</i>)			X	X	X	X	
sheepshead (<i>Archosargus probatocephalus</i>)				X	X	X	X
pinfish (<i>Lagodon rhomboides</i>)	X		X		X	X	X
silver perch (<i>Bairdiella chrysoura</i>)			X	X	X	X	
spotted seatrout (<i>Cynoscion nebulosus</i>)			X		X		
weakfish (<i>Cynoscion regalis</i>)			X	X	X		
spot (<i>Leiostomus xanthurus</i>)	X	X	X	X	X	X	
Atlantic croaker (<i>Micropogonias undulatus</i>)		X	X	X	X	X	
black drum (<i>Pogonias cromis</i>)				X	X		
red drum (<i>Sciaenops ocellatus</i>)						X	
spotfin butterflyfish (<i>Chaetodon ocellatus</i>)				X			
striped mullet (<i>Mugil cephalus</i>)						X	X
white mullet (<i>Mugil curema</i>)						X	
tautog (<i>Tautoga onitis</i>)			X	X			
lyre goby (<i>Evorthodus lyricus</i>)						X	
Atlantic cutlassfish (<i>Trichiurus lepturus</i>)				X			
Spanish mackerel (<i>Scomberomorus maculatus</i>)			X		X		
harvestfish (<i>Peprilus alepidotus</i>)			X		X		
butterfish (<i>Peprilus triacanthus</i>)			X		X		
bay whiff (<i>Citharichthys spilopterus</i>)						X	
summer flounder (<i>Paralichthys dentatus</i>)	X		X	X	X	X	
southern flounder (<i>Paralichthys lethostigma</i>)					X	X	
winter flounder (<i>Pleuronectes americanus</i>)	X			X			
blackcheek tonguefish (<i>Symphurus plagiusa</i>)				X		X	
hogchoker (<i>Trinectes maculatus</i>)		X	X				
orange filefish (<i>Aluterus schoepfi</i>)						X	
planehead filefish (<i>Stephanolepis hispidus</i>)						X	
pygmy filefish (<i>Monacanthus setifer</i>)					X		
striped burrfish (<i>Chilomycterus schoepfi</i>)	X						
northern puffer (<i>Sphoeroides maculatus</i>)			X				
Transient Decapod Crustaceans							
brown shrimp (<i>Penaeus aztecus</i>)						X	
pink shrimp (<i>Penaeus duorarum</i>)						X	X
white shrimp (<i>Penaeus setiferus</i>)						X	
daggerblade grass shrimp (<i>Palaemonetes pugio</i>)	X	X		X	X	X	X
marsh grass shrimp (<i>Palaemonetes vulgaris</i>)	X	X		X	X	X	X
lesser blue crab (<i>Callinectes similis</i>)						X	
blue crab (<i>Callinectes sapidus</i>)	X	X	X	X	X	X	X

Common name (scientific name)	MD1 ^a	MD2	VA1 ^b	VA2 ^c	NC	SC ^d	TX ^e
Number of oyster reef resident fishes	5	5	4	5	5	3	5
Number of facultative resident fishes	3		2	3	2	2	0
Number of transient fishes	10	10	26	29	25	30	9
Number of transient decapod crustaceans	3	3	1	3	3	7	4
Total number of species	21	18	33	40	35	42	18

^aFlag Pond data are from dive surveys only.

^bPiankatank data are from trawls along the reef base.

^cFisherman's Island data are from gill nets, drop nets, and trawling, as well as from diver surveys.

^dSouth Carolina data are from replicate (24-m² of oyster habitat) lift nets triggered at high slack tide and fished at low tide.

^eTexas data are from 2.6-m² drop-trap samples.

beds of SAV); and (3) transient species, which may forage on or near the reef but are wide-ranging (Breitburg, in press). Of the 79 finfish species found in surveys of oyster reefs in Maryland, Virginia, North Carolina, South Carolina, and Texas (Table 1), seven species (naked goby *Gobiosoma bosc*, striped blenny *Chasmodes bosquianus*, feather blenny *Hypsoblennius hentz*, freckled blenny *H. ionthas*, skillettfish *Gobiesox strumosus*, oyster toadfish *Opsanus tau*, and gulf toadfish *O. beta*) can be clearly identified as oyster reef residents. For these species, oyster reef habitat can be considered "essential" with a high degree of certainty. These resident gobies, blennies, toadfish, and clingfish use oyster reefs as breeding and feeding habitat and as shelter from predators. Oyster and gulf toadfish attach eggs to the underside of consolidated masses of oyster shells, while the smaller gobies, blennies, and clingfish lay eggs on the inside of recently dead oyster shells that are still articulated (Breitburg, in press). Size-based competition exists for oyster shells as nest sites, and small oyster reef residents need shells whose inner surfaces have not yet become covered with sessile invertebrates. Because of these factors, well-developed oyster reefs with natural and continuous levels of oyster mortality in all size classes are likely to provide the best supply of new nesting sites (i.e., clean, still-articulated oyster shells in a variety of sizes, including large oysters) to accommodate reproduction by high densities of all resident species (Breitburg, in press). Unconsolidated small cultch material (e.g., coal ash), large rocks, and rubble are likely to be poor substitutes for the natural reef shell matrix. In addition to the seven species listed as oyster reef residents in Table

1, descriptions of breeding habitat indicate that the seaboard goby *G. ginsburgi*, green goby *Microgobius thalassinus*, longhorn sculpin *Myoxocephalus octodecemspinosus*, Atlantic midshipman *Porichthys plectrodon*, and northern pipefish *Syngnathus fuscus* also use oyster reefs as habitat for reproduction (Hardy 1978a, 1978b; Johnson 1978; Jones et al. 1978; Martin and Drewry 1978).

In addition to the above-mentioned species that breed on oyster reefs, a much larger number of fish species (including many that are important to recreational and commercial fisheries) facultatively utilize oyster reefs and the waters directly overlying them as feeding and refuge sites. (The numbers below include only facultative residents and transients.) Studies in Chesapeake Bay (Maryland and Virginia), the Neuse River and Pamlico Sound (North Carolina), the Charleston Harbor area (Inlet Creek and Toler's Cove sites in South Carolina), and West Bay (Galveston, Texas) have identified 72 facultative resident and transient fish species in close proximity to oyster reefs through diver observations and the use of trawls, drop samplers, lift and gill nets, and fish trays and traps (Table 1, Figure 1). Species listed in Table 1 as facultative residents appear to be represented by at least some individuals that remain on the oyster reef for several months. Some species listed as transients may actually be facultative residents (exclusive of South Carolina intertidal species). However, these species are highly mobile within the reefs, and the duration of residency of individuals has not been studied. Differences in species richness (Figure 1) and composition among sites in Table 1 likely reflect differences in collection methods (see Table 1 footnotes), as well as true differences in the fish and crustacean assemblages.

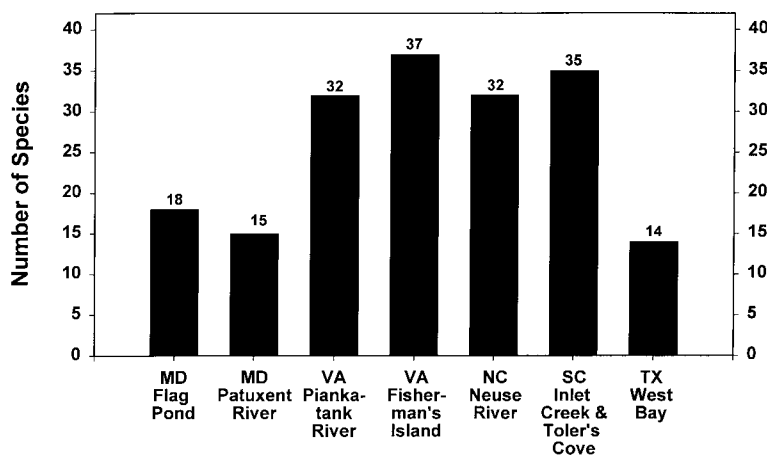


FIGURE 1.—Cumulative number of finfish species (resident, facultative resident, and transient combined) collected by site and study in association with oyster reef sampling. Overall taxonomic composition and species numbers among studies (bars) reflect sample sizes and gear type differences, in addition to biogeographic diversity and local hydrographic conditions (i.e., intertidal and subtidal conditions, tidal range, salinity, depth) from Maryland to Texas. (See Table 1 for specific site information and collection methods.)

For example, 13 species of finfish (see Table 1 for additional macroinvertebrates) were observed within 1 m of the reef surface during late spring to summer at the Flag Pond Oyster Reef in the mesohaline Maryland portion of Chesapeake Bay (D. Breitburg, the Academy of Natural Sciences, personal observations), and 10 finfish species were identified on Patuxent River oyster reefs during preliminary diving (Breitburg, personal observations), gill-net, and crab-pot surveys (Breitburg and T. Miller, University of Maryland, unpublished data). J. Harding (Virginia Institute of Marine Science, unpublished data) found 28 finfish species on Piankatank River oyster reefs in Virginia, and M. Luckenbach and J. Nestlerode (Virginia Institute of Marine Science, unpublished data) found 32 finfish species on oyster reefs at Fisherman's Island near the mouth of the Chesapeake Bay. In North Carolina, H. Lenihan (unpublished data) identified 27 fish species at oyster reefs in the Neuse River, and Coen et al. (1997, unpublished data) found 32 finfish species at two South Carolina reef sites (Table 1, Figure 1). A study in the Gulf of Mexico that quantified macroinvertebrates and finfish associated with oyster reefs identified nine finfish species from 2.6-m² drop-trap samples taken in West Bay, Galveston, Texas (Zimmerman et al. 1989; Minello 1999, this volume) (Table 1, Figure 1).

Numerous macroinvertebrates, including penaeid and caridean shrimp (primarily members of the genus *Palaemonetes* spp.) and portunid crabs also are found on Atlantic coast oyster reefs (Table 1; Zimmerman et al. 1989; Wenner et al. 1996; Coen et al. 1997). It is clear from numerous estuarine studies that grass shrimp in Atlantic and Gulf estuaries serve as a critical trophic link in both detrital and higher food webs (e.g., Adams and Angelovic 1970; Bell and Coull 1978; Morgan 1980; Anderson 1985; Kneib 1997). In Texas, as in South Carolina, stone crabs *Menippe* spp. are often collected in association with oyster habitat (Wenner and Stokes 1984; Zimmerman et al. 1989; Coen et al. 1997).

As a caveat, variability in the species list and species numbers generated from these ongoing studies is reflective of large differences in sampling intensity and sampling gear (from diver observations to seines, trawls, and lift or drop nets), in addition to biogeographic (Maryland to Texas) and local system characteristics (e.g., tidal range, position, flow, depth, salinity) among sites (see Table 1, Figure 1). More important, results of these studies illustrate the wide range of species that utilize oyster reefs and highlight the importance of determining whether reef area and other characteristics influence the size and health of fish populations other than oyster reef residents. It is given that this preliminary list of species will grow significantly with time and additional studies.

As has been seen for oysters themselves, modification of flow by high-relief oyster reefs may be important to both resident fishes and to those transient fish species using reefs as feeding habitat. Large numbers of late-stage larvae of resident fish species (particularly those of the naked goby) can be found on the down-current side of high-relief structures within oyster reefs, where reduced flow velocity allows larvae to maintain their position during high-flow portions of the tidal cycle (Breitburg et al. 1995). The heterogeneity in the flow environment created by vertical relief within reefs influences the spatial pattern of settlement of fish onto oyster reefs (Breitburg et al. 1995), the spatial pattern of predation by fish larvae, and the distribution and likely the feeding success of their predators (Breitburg, in press). Larval and juvenile naked gobies and other resident fishes are significant zooplankton predators (Breitburg, in press). These fish are also, in turn, prey for larger transient fishes including striped bass *Morone saxatilis*, which can occur in high densities within 1 m of oyster reef substrate (Breitburg, in press). For example, Breitburg (in press) observed juvenile striped bass at a density of 15.4 individuals per m² of "reef" surface in diver surveys over artificial structures (33 cm x 33 cm x 33 cm concrete cubes). The juvenile striped bass were aggregating a few centimeters over the reef surface and actively feeding on naked goby larvae congregating on the down-current side of the miniature reefs.

The interstitial spaces within the oyster reef matrix may also provide a refuge from predation for small resident fishes as they do for small oyster spat. The typical behavior observed for gobies, blennies, clingfish, and small juvenile toadfish in the presence of either a predatory fish or a sudden move by a diver is to dart into the shell matrix rather than to flee along the substrate surface or rise in the water column. Although the efficiency of this escape response has not been tested experimentally, field observations indicate that the spaces within the shell matrix of a well-developed oyster reef allow small fish to escape piscivores such as striped bass and pinfish that capture prey directly from the reef surface. Similarly, mesocosm experiments have indicated that the grass shrimp *Palaemonetes pugio* seeks refuge in a simulated oyster reef when threatened by finfish predators (Posey et al., in press). The results of Posey et al. (in press) also suggest that some decapod and finfish species, in addition to those listed in Table 1, may be facultative reef residents, moving onto reefs in response to tidal stage and predator abundance.

Differentiating between habitat that is simply utilized by facultative resident and transient finfish and crustaceans and habitat that falls under the EFH definition is important to truly determine the role oyster reefs play in the ecology of coastal systems. A number of studies are addressing this need by better defining the specific habitat requirements for resident and transient species associated with oyster reefs and examining trophic links between transient finfish and the resident fish and invertebrate assemblages. For example, studies by Coen and others and Dame and others in South Carolina, Breitburg and Miller in Maryland, and Luckenbach and others in Virginia are being conducted as of this writing (see also Coen et al. 1997, in press; Dame et al. 1997; Meyer et al. 1997; Harding and Mann, in press; Lenihan and G. W. Thayer, National Marine Fisheries Service, unpublished data; D. Meyer, National Marine Fisheries Service, personal communication).

Parallels with Artificial Reefs

Another critical issue to address in determining whether oyster reefs can be considered EFH on the basis of their use by fish is the extent to which oyster reefs result in the production of additional fish biomass rather than simply concentrating existing fish biomass. The question of concentrating biomass versus increasing regional production may be especially critical for constructed reefs and for finfish species that are targeted by commercial or recreational fisheries. As Grossman et al. (1997) pointed out, artificial reefs that concentrate biomass, but do not increase production, may be detrimental to fish populations because such reefs also concentrate fishing pressure and can increase total fishing mortality of targeted stocks. Although it may seem logical that the concentrating effect of reefs is due to their attractiveness as feeding habitat and that better feeding habitat will result in greater fish production, Grossman et al. (1997) suggested that for the majority of cases there are insufficient data to determine whether the net effect of reef construction is beneficial to finfish populations and further suggested that the effect of reef construction will depend on the factors that currently limit local fish abundance. Regional assessments of the effects of reef construction will be needed because of the open (i.e., mobile) nature of many fish populations (Carr and Hixon 1997).

Of paramount importance for determining the value of constructed reefs as EFH for reef-associated estuarine species is distinguishing between the habitat value of reefs with viable oyster populations

and more traditional artificial fishing reefs (e.g., wrecks, concrete rubble, and constructed concrete structures). The distinction here is likely to be one of degree, as virtually any hard substrate appropriately placed within Atlantic and Gulf coast estuaries will develop epifaunal assemblages that include some *C. virginica*. However, we hypothesize that fully functional oyster reef habitats will provide ecosystem services and EFH benefits that have the potential to increase regional fish production beyond increases provided by artificial reef habitats for at least three reasons:

1. In high-sedimentation environments typical of many estuaries inhabited by *C. virginica*, growth of the entire reef, via growth of individual oysters and annual recruitment, provides a mechanism for maintaining the reef in the face of sedimentation. As discussed elsewhere (Coen and Luckenbach, in press), it is doubtful that any other species within the oyster reef assemblage, including mussels (primarily *Mytilus edulis* and *Geukensia demissa*), is capable of providing sufficient structural integrity and vertical relief to overcome natural sediment deposition rates and near-bottom hypoxia (see Lenihan and Peterson 1998).
2. Living oyster reefs provide a diversity of microhabitats—both for support of oyster survival (Bartol and Mann, in press) and for nesting sites and shelter sites for resident finfish (see preceding discussion and Breitburg, in press)—that are not necessarily provided by artificial reef structures lacking high densities of oysters.
3. In some mid- and south-Atlantic coastlines with tidal ranges in excess of 1–2 m, oyster reefs provide extensive intertidal habitat that cannot be mimicked with traditional artificial fishing reefs.

Oysters are capable of growing in dense vertical clusters or hummocks (cf. Bertness et al. 1998), extending above the surrounding soft sediments and forming reefs where other epifaunal species would quickly be buried. Reef bases constructed as part of restoration efforts of materials other than oyster shell (e.g., fly or coal ash, sludge bricks, construction rubble, etc.) need to mimic both the vertical relief and interstitial space provided by mounded oyster shell to ensure that viable oyster populations can persist and that natural reef communities can exist.

Linkages with Other Types of EFH

Estuaries have long been recognized as the most productive ecosystems in the world (Peterson and Lubchenco 1997). They provide critical feeding, spawning, and nursery habitats for numerous species, including commercially and recreationally important fish, shellfish, and waterfowl. Most of these organisms are dependent upon one or more estuarine habitats (e.g., SAV, mud flats, salt marshes, oyster reefs) that are being lost or degraded at an ever-increasing rate as a result of coastal population increases and associated industrial, residential, and recreational development.

Management practices that protect habitats or mitigate for losses are often based on the assumption or recognition that key habitats are critical to nearshore ecological processes such as nutrient cycling, nursery habitat functions, and trophic stability and are important, for example, in maintaining coastal fisheries (Costanza et al. 1997; Peterson and Lubchenco 1997). The question of relative habitat value is important given the frequent legal mandate to protect or restore coastal habitats that have undergone significant changes as a result of development. Throughout most estuaries, multiple habitats (e.g., mud, SAV and emergent vegetation, oysters) exist in a mosaic, providing a complex environment for associated mobile species (Bell et al. 1991 and papers therein) and recruiting sessile flora and fauna. However, the relative ranking in value and contribution of each different nearshore habitat to ecosystem functions and overall biodiversity remain largely undetermined (e.g., Heck and Wetstone 1977; Weinstein and Brooks 1983; Wilson et al. 1987, 1990; Thomas et al. 1990; Rozas and Minello 1997). In addition to these landscape issues, mobile organisms typically occupy a suite of habitats during their life cycles, and we are just beginning to evaluate these linkages (e.g., Abele 1974; Bray et al. 1981; Parrish 1989; Zimmerman et al. 1989; Ambrose and Anderson 1990; Fitz and Wiegert 1991; Barshaw et al. 1994; Posey and Ambrose 1994; Heck and Coen 1995; Heck et al. 1997; Irlandi and Crawford; 1997; Posey et al., in press).

For oyster reef habitat, whether intertidal or subtidal, we have little comparative data with which to examine linkages with other habitats. For example, in South Carolina, sea grasses are absent, but there is abundant salt-marsh habitat interspersed with extensive tidal mud flats and oyster reefs. The importance of each of these dominant intertidal habitats has been indicated through independent efforts us-

ing very different sampling gear. Which habitats are utilized or required by which species is unclear. Anecdotal information and recent quantitative studies (Table 1; Wenner et al. 1996; Coen and Luckenbach, in press; Coen, unpublished data) for South Carolina indicate that many fishes (e.g., anchovy and silversides) are attracted to oyster reefs because the reefs' habitat structure provides a refuge from ecologically and commercially important fish predators (e.g., spotted seatrout *Cynoscion nebulosus* and flounders). These large predators, along with sheepshead *Archosargus probatocephalus*, black drum *Pogonias cromis*, and red drum *Sciaenops ocellatus* (see Table 1), migrate into creeks on flood tides to feed on small crabs and shrimp that reside in and around reef structure in large numbers (Coen, unpublished data). Quantitative sampling on the vegetated intertidal areas has shown that penaeid shrimps, flounders, blue crabs *Callinectes sapidus*, and other important species make regular tidal excursions across the flooded vegetated salt marsh (Hettler 1989; Rozas 1993; Kneib and Wagner 1994; Peterson and Turner 1994; Irlandi and Crawford 1997; Minello 1999; D. Allen, University of South Carolina, unpublished data; M. Posey, University of North Carolina Wilmington, unpublished data). Clearly, intertidal oyster reefs and salt marshes together provide a valuable set of structured habitats for juveniles of many important fish species such as sheepshead, gag grouper, and snapper, as well as stone and blue crabs and penaeid shrimps (Table 1; Wenner et al. 1996; Coen, unpublished data).

Similarly, sampling on subtidal and intertidal Chesapeake Bay oyster reefs and adjacent habitats has begun to elucidate transient utilization patterns by both finfish and decapod crustaceans (Table 1; Nestlerode, unpublished data). At Fisherman's Island, Virginia, the development of extensive sea grass beds (*Zostera marina* and *Ruppia maritima*) adjacent to experimental reefs is providing an opportunity to track community development in both habitat types (Luckenbach et al. 1997). Underwater video is currently being used to characterize movements of transient species between reefs and adjacent habitats (Nestlerode, unpublished data). In a coastal lagoon in Magothy Bay, Virginia, J. Wesson with the Virginia Marine Resources Commission and R. Orth and colleagues from the Virginia Institute of Marine Science have recently initiated a project involving experimental construction of oyster reefs and eel-

grass habitats individually and in combination to evaluate community development and utilization of these structured habitats.

Finally, few studies and associated models have incorporated the contribution of oyster larvae to zooplankton biomass. The effects of significant ecosystem shifts (for example, in Chesapeake Bay) from oyster-dominated systems with enormous numbers of oyster larvae as a food source to present conditions dominated by gelatinous secondary consumers are unclear (Newell 1988; Ulanowicz and Tuttle 1992; Dame 1996). Future research needs to evaluate the potential linkage between oyster larvae and zooplankton biomass.

Current and Future Management of Oyster Habitat

Historically, oyster habitat management has not been one of the primary goals of resource managers attempting to maintain oyster harvests (Lenihan and Peterson 1998; Lenihan and Micheli, unpublished data). However, with improved understanding of the added ecosystem services derived from these biogenic habitats (see above and Daily 1997; Peterson and Lubchenco 1997), we sense that a shift is beginning to occur in how we view, manage, and restore molluscan-dominated systems (Frankenberg 1995; Lenihan and Peterson 1998; C. Peterson, University of North Carolina, personal communication).

Three basic management and restoration approaches are available to resource managers: (1) fisheries restrictions on existing reefs; (2) substrate additions; and (3) stock enhancement through active transplanting of oysters. The first of these approaches has generally not proven to be sufficient to maintain either oyster standing stocks or reef integrity. Recent closure of the oyster fishery throughout most of the Virginia portion of Chesapeake Bay has resulted in increases in oyster standing stocks in the area, but the closure has not been sufficient, at least in duration, for the development of reefs with significant three-dimensional relief (J. A. Wesson, Virginia Marine Resources Commission, personal communication).

The addition of oyster shell and (occasionally) alternative substrates is a widespread management tool designed to replace substrate extracted as part of the fishery or to extend oyster recruitment into new areas (reviewed in Luckenbach et al., in press).

This approach has generally been associated with a put-and-take fishery. In the absence of harvest restrictions, it makes little economic sense to restore oyster reef habitat by adding substrate beyond that necessary to achieve market-size, 2-to-3-year-old oysters.

In some areas such as Connecticut's Long Island Sound, the transplanting of wild oysters to enhance oyster resources has been successful, but the emphasis has been on improved growth to market size rather than reef habitat restoration (Volk, personal communication). Hatchery-produced oysters, set onto bags of shell and planted in the field, are being used to supplement natural recruitment of oysters in Maryland and Louisiana (Supan et al., in press; D. Merritt, University of Maryland, personal communication). Again, this transplanting effort has been directed toward a short-term put-and-take fishery. Current management approaches in Virginia involve all three of the above elements, including broodstock enhancement programs using both wild and hatchery-reared stocks. These enhancement programs concentrate broodstock with desirable traits (disease tolerance and rapid growth) onto reef bases with adequate three-dimensional relief (constructed from shell plantings) and protect them from harvest as broodstock sanctuaries. This strategy is intended to restore viable oyster populations and functioning reef habitats while supporting oyster fisheries in adjacent areas through enhanced oyster recruitment.

Areas where shellfish harvesting is prohibited or restricted owing to public health concerns may provide an opportunity to create refuge areas for both oysters and reef-associated species. We contend that protecting and restoring shellfish habitat in these areas may be desirable due to the habitat's intrinsic worth as both habitat and larval and broodstock reserves (cf. Whitlatch and Osman, in press). Recent research also suggests that many areas that are closed due to human health concerns support resident and transient finfish and crustacean associations equivalent to those of open areas (Coen et al. 1997; Coen and Luckenbach, in press; Coen et al., unpublished data).

Our expectation is that establishing reef sanctuaries, whether in areas closed to harvesting (see above) or in areas classified as either open or restricted, may, among other benefits, serve as sources of oyster larvae for surrounding exploited areas. This activity has recently been suggested for Virginia

waters (Wesson, personal communication; see also Whitlatch and Osman, in press). However, the establishment of sanctuaries raises difficult questions. Ultimately, we will have to weigh derived ecosystem services against the resource's economic value (Costanza et al. 1997; Daily 1997; Kaufman and Dayton 1997; Lenihan and Micheli, unpublished data). Fisheries interests have considerable political support in some regions (e.g., Chesapeake Bay) and in most cases are the principal source of funding for oyster reef restoration efforts (cf. New Chesapeake Bay Reef Programs). Balancing short-term exploitation against the need to establish sustainable and functioning reefs poses a formidable challenge.

Future Needs

Manipulative studies of the types described in this chapter will be required to evaluate the individual and linked contributions of various estuarine habitat types to the maintenance of ecosystem services and to establish the relative importance of oyster reef habitat in these systems. Results from our work in South Carolina, Virginia, and Maryland and by others in North Carolina make it clear that considerable work must still be done to establish appropriate metrics for evaluating the value of oyster habitat as EFH and associated links with other estuarine habitats that may also serve as EFH. Such evaluations will require further research on natural reefs to clarify ecological functions, critical species, functional groups, and trophic structure interactions. Continued characterization of the development of "restored" reefs to establish successional trajectories and appropriate time scales will also be required. The identification of critical habitat components for other target species must be a focal point of these efforts. Currently we have very little data for natural reef systems. Detailed analyses of trophic links to transient finfish species are currently underway in several studies (e.g., Harding and Mann, in press; Coen, unpublished data; Lenihan and Thayer, unpublished data; Luckenbach, unpublished data; Miller and Breitburg, unpublished data) and should provide critical information on the value of oyster reef habitats to commercially exploited finfish.

Achieving a working balance between resource extraction and habitat function will require the development and testing of alternative harvest practices that permit extraction of oysters after some

developmental period while maintaining habitat services as discussed above. Currently, we do not know whether extraction and habitat function are compatible (Burrell et al. 1991; Kaufman and Dayton 1997; Lenihan and Micheli, unpublished data). Implicit in this uncertainty is the need for adaptive management approaches that incorporate monitoring and research-based information into restoration efforts and management decisions (Grumbine 1994; Christensen et al. 1996; ESA 1998; Lenihan and Peterson 1998).

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