Atlantic States Marine Fisheries Commission

The Importance of Habitat Created by Molluscan Shellfish to Managed Species along the Atlantic Coast of the United States

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Working towards healthy, self-sustaining populations of all Atlantic coast fish species or successful restoration well in progress by the year 2015

ASMFC Habitat Management Series #8

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I. INTRODUCTION

Along the Atlantic coast of the continental United States, shellfish habitats occur in estuaries, near-shore coastal waters, and offshore on the continental shelf (Shumway and Kraeuter 2004), and provide numerous ecological services to these systems. Both bivalve and gastropod molluscs form these types of shellfish habitats. Two hinged 'valves' or 'shells' characterize bivalve shellfish (e.g., clams, mussels, and oysters). Gastropods (or snails) are sometimes called 'univalves' because they have a single, typically coiled shell. For both bivalves and gastropods, the shell structure, which functions as an exoskeleton, is composed of a matrix of calcium carbonate and organic materials, and is secreted by the underlying soft mantle tissue.

Many shellfish species are consumed by finfish or other vertebrate and invertebrate predators (e.g., mammals, birds, finfish, other molluscs). Some shellfish support major commercial and recreational fisheries, and a subset create important habitats, particularly when they occur at high densities. The habitats created by molluscs can be classified into three major types: (1) reefs (veneer of living and dead animals), (2) aggregations (living and dead), and (3) shell (dead) accumulations (often called 'shell hash'). Some habitats can be grouped into either category 2 or 3, depending on the relative abundance of dead shell versus live organisms.

The eastern oyster (*Crassostrea virginica*) and blue mussels (*Mytilus* spp.) are two major examples of reef-forming shellfish that occur along the Atlantic coast (Sellers and Stanley 1984; Burrell 1986). Before mechanized harvesting techniques were used, subtidal oyster reefs in some estuaries probably extended as much as several meters above the bottom, forming complex three-dimensional structures that provided habitat for finfish and invertebrates (Galtsoff 1964; Dame et al. 1984a, 1984b; DeAlteris 1988; Kennedy and Sanford 1999; CBP 2001; Dame and Libes 1993; Smith et al. 2003). Today, subtidal oyster reefs rarely extend more than a few decimeters above the bottom; nonetheless, they provide important habitat for economically and ecologically important species (Bahr and Lanier 1981; Sellers and Stanley 1984; Breitburg 1988, 1989, 1991, 1999; Coen et al. 1999b; Posey et al. 1999; Peterson et al. 2003). Artificially enhanced oyster grounds can create extensive acres of "planted" beds, either with cultch for spat collection, or the transfer of variously aged oysters for grow out (L. Stewart, University of Connecticut, personal communication).

Other shellfish that cement together to form reef-like structures can be found in a family of gastropods known as the Vermetidae (Safriel 1975). Alternatively, the sea scallop (*Placopecten magellanicus*) is an example of a species that does not form reefs, but often occurs in aggregations of adequate density to provide habitat for other species (Langton and Robinson 1990; Stokesbury 2002).

A third type of shellfish habitat is formed by ocean quahog (*Arctica islandica*), surf clam (*Spisula solidissima*), and other abundant bivalves (e.g., *Mercenaria* spp. and *Mya arenaria*), whose shells can persist long after the inhabiting organism has perished. Sometimes abandoned shells accumulate on the seabed of the continental shelf in sufficient quantities to provide significant structure and habitat for a variety of organisms (Dumbauld et al. 1993; Auster et al. 1995; Palacios et al. 2000; Steimle and Zetlin 2000; Stoner and Titgen 2003). During a lobster research study on post-larval habitats, divers on the shoals off of northern Long Island reported concentrations of *Spisula* sp. shell accumulations (more than 20 cm in depth) along the slopes, providing habitat for juvenile lobster, crabs, and benthic fishes (Lund et al. 1973). These four types of shellfish environments combine to provide significant amounts of habitat, particularly for juveniles of many fish species.

The four types of shellfish habitats (reefs, aggregations, shell accumulations, and cultured ground) show great variation in physical characteristics and their relationship to managed species. Although there is rich literature (published and unpublished) that demonstrates the importance of all four habitat types to ASMFC-managed species, other structure-forming organisms, such as seagrasses, have garnered much of the attention of management agencies. In part, this is due to the almost exclusive management perspective of shellfish as a food resource for humans. Recently, however, the broader ecological value of shellfish has begun to gain more universal recognition (Luckenbach et al. 1999). The result has been an ongoing expansion of the focus of shellfish research and management.

Therefore, in addition to an examination of the direct relation of shellfish habitat to managed species, this document also deals with the broader ecological context of shellfish habitat, because management decisions often require that type of information. Worth noting here are recent papers generated from work supported by the National Center for Ecological Analysis and Synthesis (NCEAS at UCSB) on important nearshore habitats, which suggest that our understanding of these habitats as nursery areas is still far from complete (Beck et al. 2001, 2003).

Important Characteristics of Shellfish Habitat

Most, if not all, state and federal fisheries management agencies did not view shell bottom habitats as essential fish habitat (EFH) until the 1990s. For example, Street et al. (2005) provide an excellent discussion of 'shell bottoms', which they define as, "living or dead oysters (*Crassostrea virginica*), hard clams (*Merceneria merceneria*), and other shellfish." For the purpose of this report, the ASMFC Habitat Committee has defined 'shellfish habitat' (Figure 1) as:

> *Intertidal and/or subtidal habitat generated by living molluscan shellfish and/or dead associated shell in continuous or discrete beds, including, but not limited to, bivalve habitats, such as oyster reefs and mussel beds, forming three-dimensionally complex structure in an otherwise two-dimensional environment (e.g., within soft sediment, rocky shores, or rubble).*

Shellfish habitat—whether it is a living assemblage or an accumulation of dead shells—provides hard substrate for the attachment of many species that would not be present in areas consisting only, or mainly, of soft sediments (Figure 1). The overall ecological result is greatly enhanced biodiversity in shellfish habitat compared to surrounding areas of the seabed. For example, in his classic study on eastern oyster reefs, Wells (1961) found over 300 species of invertebrates that were largely restricted to the reef structure or other hard-bottom habitats, and thus did not typically occur in adjacent non-reef habitat.

Shellfish habitat is also characterized by a greater amount of vertical relief in comparison to the surrounding seabed. This enhanced vertical relief is of major importance, with implications for assessing habitat value for managed species and for development of management policy. For example, an oyster or mussel reef protruding only several centimeters above the bottom represents, in terms of fluid mechanics, a "roughness element." Roughness elements substantially affect water flow, which creates larger zones of turbulence, and alters hydrodynamics and material transport (Officer et al. 1982; Dame 1996; Kennedy 1996; Coen et al. 1999b; Luckenbach et al. 1999; Nelson et al. 2004). Changes in these physical processes directly influence recruitment, growth, and other biotic processes of the shellfish and other organisms (e.g., finfish) that live on the reef (Zimmerman et al. 1989; Kennedy and Sanford 1999; Breitburg 1999; Lenihan 1999; Coen et al. 1999b; Luckenbach et al. 2005). Therefore, policy development should include a consideration of the impacts of fishing and other regulated activities on structural components of shellfish habitat.

Shellfish habitats that consist of living molluscs also represent an important food source for many species of fish and invertebrates. For example, oysters are consumed by a wide range of predators, including rhynchocoel worms, gastropod drills, starfish, conch, crabs, finfish, and birds (Galtsoff 1964; Bahr and Lanier 1981; Blundon and Kennedy 1982; White and Wilson 1996; Newell et al. 2000). Consequently, habitats that include live shellfish provide a direct and indirect food source for many species in marine and estuarine food webs.

In summary, these four characteristics of shellfish habitat—hard substrate, vertical structure, food, and water quality regulation—result in a significant enhancement of overall habitat value for many species of Atlantic shelf, coastal, and estuarine waters. Section II provides details on these characteristics, the ecological services they provide, and the major shellfish species involved.

II. HABITAT-FORMING SHELLFISH AND THEIR ECOLOGICAL VALUE

A) Reef-forming Species

In the western Atlantic, oysters, mussels, and one genus of gastropod build three-dimensional structures that are commonly called reefs (Figure 1). Wood (1998, 1999) reviews the term 'reef', and discusses its origin and those taxa and concepts that relate to reefs. The term derives from a Norse term 'rif', or hazardous 'rib' of sand, rock, or biologically generated substrate near the surface. Wood (1999) includes the following as extant reef producers: corals, coralline and calcareous algae, sabellariid and serpulid polychaetes, oysters, vermetid gastropods, bryozoans, sponges, and stromatolites (i.e. Cyanophytes). Other terms such as "bars" and "beds" also refer to reef structures that are created by the organisms themselves. Holt et al. (1998) define 'biogenic reefs' as:

> *solid, massive structures which are created by accumulations of organisms, usually rising from the seabed, or at least clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed. The structure of the reef may be composed almost entirely of the reef building organism and its tubes or shells, or it may to some degree be composed of sediments, stones and shells bound together by the organisms.*

Our focus here includes many shellfish species (e.g., mussels, dense clam beds) that may be classified somewhere between 'non-reef' and 'reef-forming" biotopes. Holt et al. (1998) try to characterize these biotopes, but this is a difficult task. Furthermore, researchers often refer to the structure that a species generates as a 'habitat', 'biotope' or 'biogenic reef'. We focus on species that create unique and definable areas that are different from the surrounding unstructured sediments.

Although many species typically occur on shellfish reefs, the main structural component is formed by the attachment of many individual shellfish to each other. At least three species of oysters occur along the Atlantic coast, in addition to several mussel species and other molluscs (e.g., vermetid gastropods) (Abbott 1974). Of these, only the Eastern (or American) oyster (*Crassostrea virginica*), blue mussel (*Mytilus edulis*), and horse mussel (*Modiolus modiolus*) typically form reefs along the Atlantic coast (Figure 1). Currently, in the Chesapeake Bay and elsewhere, there is uncertainty over whether a non-native oyster from the Pacific (*C. ariakensis*) can serve both as a 'reef builder' and suitable fisheries resource substitute for *C. virginica* (NRC 2004; Ruesink et al. 2005).

Eastern oyster (*Crassostrea virginica*)

The eastern oyster's range extends from the Gulf of St. Lawrence to Key Biscayne, and south to the West Indies and the Yucatan Peninsula in Mexico (Galtsoff 1964; Burrell 1986; Kennedy et al. 1996; MacKenzie et al. 1997a). The eastern oyster is mainly an estuarine organism, but does occur in some near-shore coastal waters. These oysters grow sub-tidally throughout most of their range, but from southern North Carolina to northeastern Florida they occur predominately in the intertidal zone (see Figures 1 and 2) (Bahr and Lanier 1981; Kennedy et al. 1996; Kennedy and Sanford 1999; Burrell 1986, 1997; Coen and Luckenbach 2000;

Luckenbach et al. 2005). Although they occur to a depth of 30 m, the oyster's primary habitat is in shallow water less than 6 m, or intertidal (1 m to 5 m) from North Carolina to Florida. A typical feature of *C. virginica* is their extremely variable shell morphology (Galtsoff 1964; Carriker 1996; Kent 1992). Oysters have indeterminate growth; in historical times, prior to the influence of harvesting and other biological and anthropogenic factors, they often grew to sizes significantly greater than what we see today (20 cm or larger shell height).

Oysters initially mature as males at an early age and then change sex to spawn primarily as females (Galtsoff 1964; Kennedy et al. 1996). Adult oysters are stimulated to release gametes (eggs or sperm) into the water column by increasing water temperatures. Subsequently, fertilization occurs and free-swimming larvae develop, which drift with the currents for up to three weeks before settling to the bottom and cementing permanently to a hard substrate. The preferred substrate for larval settlement is oyster shell, an adaptation that assures the proximity of other oysters, which is essential for successful future reproduction. Oysters are attached to the substrate or to each other by the left valve, which tends to be thicker and more deeply cupped than the right valve (Galstoff 1964; Kennedy et al. 1996; Soniat et al. 2004). Thus, dense reefs are formed by the setting of successive generations of oysters on the shells of their predecessors (Figure 1). In some places, oyster shell can be several meters deep or more with live animals only on the surface layer.

Long-term reef development is a complex process that involves interactions among a variety of physical and biotic factors (Bahr and Lanier 1981; Kennedy and Sanford 1999; Coen and Luckenbach 2000). In southern Atlantic waters, a reef-like structure may be achieved in three to five years, but in northern waters the process is apparently much slower. The long-term dynamics of oyster reefs have not been well studied, but some reefs in the Chesapeake Bay have persisted for millennia (Smith et al. 2003). In part because estuaries are geologically ephemeral, oysters must cope with changes in sea level, sediment, and climate. In contrast, within the past 50 years, some intertidal reefs in Florida have been completely destroyed and displaced landward by dredging and/or boat wakes (Figure 3). Hurricanes have also been implicated in a few instances; for example, in the destruction of the windrows of shell in surf troughs along the Florida coast (Livingston et al. 1999, Grizzle et al. 2002; Walters et al. *in press*). Elsewhere, hurricanes may have significant impacts on shellfish habitats, particularly in shallow waters (Andrews 1973; Munden 1975; Lowery 1992; Dugas et al. 1998; Livingston et al. 1999; Perret et al. 1999).

Bartol and Mann (1997) observed an increase in oyster survival when oysters settled in the interstitial spaces between shells below the reef surface. Additionally, vertically growing oysters in clusters on intertidal reefs provide oysters with a way to cope with siltation, so that they are not smothered (Coen et al. 1999a; Giotta 1999).

Crassostrea virginica reefs typically support a host of other associated organisms that are not found in surrounding sand or mud habitats (e.g., over 300 species on North Carolina reefs (Wells 1961) and over 135 species on South Carolina reefs (Coen et al. 2006a)) (Stanley and Sellers 1986a, 1986b; Coen et al. 1999b; Jackson et al. 2001; Lenihan et al. 2001; Newell 2004; Soniat et al. 2004). Recent work has attempted to quantify the contribution of oyster reefs to ecosystem functioning (Peterson et al. 2003; Peterson and Lipcius 2003; Grabowski and Peterson 2007). Oysters create complex habitats utilized by fish, crustaceans, other bivalves (e.g., mussels), and numerous other invertebrates, birds, and mammals (Coen et al. 1999b; Sanders et al. 2004). These habitats often rival salt marshes in terms of abundance of harbored organisms

(Glancy et al. 2003). Oyster habitats also filter significant quantities of water, potentially improving water clarity/quality (Dame 1996; Cressman et al. 2003; Nelson et al. 2004; Newell 2004).

One of the most ecologically important and common estuarine invertebrates associated with oyster reef habitats are members of the genus *Palaemontes* (grass shrimp) (Table 2) (Anderson 1985). *Palaemontes* spp. are a major food item for many managed fish species (Williams 1984; Collette and Klein-MacPhee 2002). Throughout their range, these small, abundant decapod crustaceans (*P. vulgaris* and *P. pugio*) are often found in densities exceeding 150 individuals/m^2 (Coen et al. 1999a, 2006a).

Caribbean mangrove oyster (*Crassostrea rhizophorae*)

The Caribbean mangrove oyster is restricted to the south Atlantic and Gulf coasts (Abbott 1974) and does not typically form reefs. *C. rhizophorae* is well adapted to the warmer tropical and subtropical temperatures in its native range (Bacon et al., 1991). *C. virginica* and *C. rhizophorae* oysters are closely related species (Buroker et al. 1979; Hedgecock and Okazaki 1984). Mangroves are typically the primary 'hard' substrate for attachment of these often common and flat oysters. Numerous other species of 'mangrove oysters' have been described, all in the genus *Crassostrea.* For all these species, information is extremely limited, with even less known on how they may enhance habitat complexity along the southern coast of Florida. *C. rhizophorae* is commercially important, can grow to marketable size (50 -70 mm shell height) in 4 to 8 months (Rodriguez and Frias 1992), and is currently cultivated in aquaculture facilities in the Caribbean (Littlewood 1988; Bacon et al. 1991; Newkirk and Field 1991).

Currently, there is very little information on the Caribbean mangrove oyster's ecology (i.e. densities, filtering, etc.) or potential habitat value for other Florida mangrove-related species. However, it must be noted that the species adds considerable habitat to the recognized three-dimensional mangrove fish nurseries of the Carribbean (L. Stewart, University of Connecticut, personal communication). Presumably Caribbean mangrove oyster reefs are fouled by many different planktonic plant and animal species, thus providing a critically needed substrate for attachment.

In large part resulting from recent work on *Crassostrea ariakensis* in North Carolina (Grabowski et al. 2003, 2004; NRC 2004; Bishop et al. 2006; Carnegie et al. 2006; R. Carnegie, Virginia Institute of Marine Science, personal communication), researchers have begun to examine the dynamics of poorly studied native oyster species, such as the crested oyster (*Ostreola equestris*). Additional attention has been drawn to novel or endemic *Bonamia* spp. (newly described or observed) that may cause diseases in native or non-native species, or act as parasite reservoirs (Bishop et al. 2006; Carnegie et al. 2006; R. Carnegie, Virginia Institute of Marine Science, personal communication).

Estuarine and marine mussels

Reef-forming mussels include the *Mytilus* spp. complex (*M. edulis* and *M. trossulus*) and the horse mussel (*Modiolus modiolus*). *Mytilus* spp. (most widely recognized blue mussels) occur from Labrador to Cape Hatteras, North Carolina, on the western Atlantic coast (Abbott 1974; Suchanek 1978, 1985; Gosling 1992, 2003; Albrecht 1998; Newell 1989; Witman and

Sebens 1988; Witman and Dayton 2001; Hellou and Law 2003). In many areas, *M. edulis* and *M. trossulus* are sympatric and hybridize (Riginos and Cunningham 2005). Additionally, the occurrence of M*ytilus galloprovincialis* (originally from the Mediterranean and now cultured throughout Europe and China) and a west coast species, *Mytilus californianus*, further complicate systems as invaders in many areas (McDonald and Koehn 1988; Varvio et al. 1988; Lobel et al. 1990; Seed 1992, 1995; Geller et al. 1994; Suchanek et al. 1997; Riginos and Cunningham 2005).

Blue mussels (*Mytilus* spp.)

Mytilus spp. occur mainly in shallow coastal waters and estuaries, and are most commonly considered a member of the fouling community because they are often found on rocks, pilings, and other hard substrates (King et al. 1990; Mathieson et al. 1991; Leichter and Witman 1997; Bertness 1999; Witman and Dayton 2001). In many areas mussels play an important role in benthic community structure (Bayne 1976; Witman 1985, 1987; Asmus and Asmus 1991; Lesser et al. 1991; Dame 1993, 1996; Hild and Günther 1999; Norén et al. 1999; Davenport et al. 2000). In some areas mussels also form dense reefs on hard bottom or on soft sediments in the intertidal and subtidal zones (Newell 1989; Nehls and Thiel 1993; Seed and Suchanek 1992; Seed 1996; Côté and Jelnikar 1999; Cranford and Hill 1999).

Blue mussel reef formation and development have not been well studied, but they are recognized as being important food and habitat providers for many species (Tsuchiya and Nishihira 1985, 1986; Witman 1985, 1987; Newell 1989; Asmus and Asmus 1991; Seed 1996; Reusch and Chapman 1997; Ragnarsson and Raffselli 1999). Mussel consumers include crabs, lobsters, starfish, whelks, fish (e.g., tautog), and birds (e.g., ruddy turnstone, American and European oystercatchers) (Marsh 1986; Meire and Ervynck 1986; Raffaelli et al. 1990; Marsh and Wilkinson 1991; Nol and Humphrey 1994; Nagarajan et al. 2002; Sanders et al. 2004). Mussel reefs perform essentially the same functions as oyster reefs; they provide food, filtration, benthic-pelagic coupling, and physical habitat (Verwey 1952; Suchanek 1978, 1985; Wildish and Kristmanson 1984, 1997; Witman and Suchanek 1984; Dame 1996; Smaal and Hass 1997).

Underwater photography documented the extensive use of mussel beds for lobster burrow shelters on soft mud substrate and within boulder habitats (Stewart 1972). Additionally, Auster et al. (1995) noted that many aquatic species utilize large "mats" of mussels in Long Island Sound in depths exceeding 33 m. When the mussel populations decline, they leave shell behind, which becomes the dominant habitat feature. Hence, both live reefs and shell accumulations are important habitat.

Additionally, a study using remotely operated vehicles (ROV) demonstrated that juveniles of many species use the shell accumulations (or windrows), including scup, American lobster, Atlantic rock crab (*Cancer irroratus*), Jonah crab (*Cancer borealis*), and long-finned squid (*Loligo pealei*) (Auster et al. 1995). When the shell accumulations were no longer present, the species associated with this habitat were absent or seen in lower densities.

Horse mussel (*Modiolus modiolus*)

The horse mussel has a geographic distribution similar to the blue mussels, but occurs mainly in deeper waters on the continental shelf; however, it can be found in intertidal pools or attached to laminarian holdfasts (Holt et al. 1998). It is a widespread mussel, found throughout the northern hemisphere from the White Sea and Norway, off the Faroes and Iceland to at least as far south as the Bay of Biscay and occasionally North Africa. It is also found from Labrador to North Carolina in the Atlantic and from the Bering Sea south to Japan and California in the Pacific. It most commonly occurs partly buried in soft sediments, or attached by byssal threads to hard substrates where it forms clumps or extensive beds (or reefs) that vary in size, density, thickness, and form (Holt et al. 1998, Wildish et al. 1998).

Horse mussel recruitment is often low and may be variable in some populations (JNCC UK 1999). *M. modiolus* is a long-lived species, with some individuals living for 25 years or more. Juvenile *M. modiolus* are heavily preyed upon, especially by crabs and starfish, until they are 3 to 6 years old, at which point they normally reach a size refuge from most of their native predators.

American horse mussel (*Modiolus americanus*)

The American horse mussel is a common mussel that often forms dense associations within seagrass habitats (Figure 1a- Plate C) (Peterson and Heck 1999, 2001a, 2001b). It ranges from South Carolina to the Gulf of Mexico and south to Brazil; it is also found in Bermuda. Adults can reach 100 mm shell height and they occur from the intertidal to approximately 6 m water depth. The American horse mussel can be found in densities as high as 2,000 individuals/m^2 with mean densities reaching 625 individuals/m^2 (Valentine and Heck 1993). However, these aggregations of American horse mussels are typically quite patchy (L.D. Coen, personal observation). Little is known about the broader ecological importance of the facultative mutualistic association of seagrass and shellfish, but work in St. Joe Bay, Florida in dense seagrass beds has shown a more complex interaction between these abundant filter-feeders and the *Thalassia* beds within which they reside. Specially, the mussels increase seagrass productivity through their filtering activities, changing nutrient availability through mechanisms such as biodeposition and reducing epiphyte loads on seagrasses (L. Coen, personal observation).

Ribbed mussel (*Geukensia demissa*)

The ribbed mussel is a relatively large mussel, growing to nearly 100 mm shell height (Figure 1). The ribbed mussel is found in coastal waters from the Gulf of St. Lawrence to Texas. It is common on both subtidal and intertidal oyster reef habitats (Van Dolah et al. 1999; Coen et al. 2004b; Luckenbach et al. 2005) and in salt marsh (Bertness 1980, 1984; Lutz and Castagna 1980; Bertness and Grosholz 1985). Unlike oysters, ribbed mussels have the ability to reattach if dislodged, which makes this species better able to adapt following a disturbance event.

The basic biology of the ribbed mussel is well understood, but little is known about its habitat value either alive or as dead articulated shells (Lent 1969; Seed 1980; Brousseau 1984; Kraus and Crow 1985; Hilbish 1987; Lin 1989a, 1989b, 1990, 1991; Wilbur and Hilbish 1989; Kemp et al. 1990; Langdon and Newell 1990; Sarver et al. 1992; Stiven and Gardner 1992; Franz 1993, 1996, 1997, 2001; Nielsen and Franz 1995; Kreeger and Newell 2000). Ribbed mussels attach by byssal threads to any hard substrate (like oyster shells and cordgrass stems) and protrude above the surface. Typically, ribbed mussels occur embedded in and amongst salt marsh sediments attached by byssal threads to each other and/or to *Spartina* spp. stalks.

Ribbed mussels occur throughout the mid- to low-intertidal regions in most southeastern estuaries. Upper intertidal limits are determined by both exposure to high temperatures and limited food availability during longer periods of tidal exposure. Lower intertidal limits are determined by the availability of effective refuge, mainly from crab predators. Although growth rates decline at higher shore levels, this is offset by increased survival (Bertness 1980; Bertness and Grosholz 1985; Stiven and Gardner 1992; Franz 2001).

A large literature exists for ribbed mussels associated with salt marsh habitats on the east coast of the United States; however, much less is known about this mussel's association with oyster reefs. Researchers in South Carolina and Virginia (Coen et al. 1999a; Coen and Luckenbach 2000; Luckenbach et al. 2005) have noted large numbers of ribbed mussels often associated with intertidal and subtidal oyster reef habitats. In South Carolina, there are *G. desmissa* densities of over 500 individuals/m^2, cohabiting areas with one or more smaller (2.5 to 5 cm) mussel species (e.g., scorched mussel (*Brachidontes exustus*) and hooked mussel (*Ischadium recurvum*)). Scorched and hooked mussels can also occur at high densities, often exceeding ribbed mussel densities (L. Coen, personal observation). For example, at some restored South Carolina intertidal oyster sites, *B. exustus* densities exceeded 4,900 individuals/m^2 and *I. recurvum* densities reached 500 individuals/m^2. As a result of these high densities of individuals, mussels can be a significant nuisance species at many Gulf of Mexico oyster reef sites (Figure 1b- Plate B).

Green mussel (*Perna viridis*)

The green mussel is a recent invader to the Caribbean, Florida (Benson et al. 2001; Baker and Benson 2002), and Georgia (Power et al. 2004), reaching lengths up to 171.5 mm (J. Fajans, University of Florida, personal observation). This species should not be confused with two morphologically similar alien species, *P. perna* and *P. canaliculus* (Siddall 1980; Benson et al. 2001; Ingrao et al. 2001). Although the green mussel is overgrowing oyster reefs in Florida (Figure 4), and becoming a serious fouling problem in Florida and Georgia, it may ultimately generate a complex and important habitat not previously observed in the southeast (J. Fajans and S. Baker, University of Florida, personal communication). Recent (October 2006) collections in Charleston, South Carolina (D. Knott, South Carolina Department of Natural Resources, personal observation), collected *P. viridis*, resulting in a new northern range extension for this non-native fouling mussel species.

Gastropods of the family Vermetidae

The only habitat-forming snails on the Atlantic coast are species in the family Vermetidae. Vermetid snails cement themselves together to form dense reefs in intertidal and shallow subtidal waters from southern New England (rarely) to the tropics (Shier 1969; Safriel 1966, 1975; Abbott 1974; Safriel and Ben-Eliahu 1991; Dame et al. 2001). These uniquely cemented gastropods feed using a mucous net (video available at http://www.mbayaq.org/video/video_snailnet_feeding_qt.asp).

Worldwide vermetid snails form an often-conspicuous group of sessile gastropods living in shallow tropical and temperate reefs, commonly constructed on *Crassostrea virginica* shell accumulations. In southwestern Florida they extend intermittently as far north as Sarasota

(Figure 5). In addition, some researchers have reported that they consider the species that was found in the Ten Thousand Islands area of southwestern Florida extinct, as the reefs were formed during the last interglacial period that drowned the beach ridges that make up the present-day islands.

There are a number of reef-forming vermetid species in Florida waters. The most common Florida species of vermetid snail, *Dendropoma corrodens*, is a small (10 mm) entrenching and encrusting species that is extremely abundant in the Florida Keys. Vermetid reef formation is restricted to the west coast of Florida, involving gastropods of the genus *Petaloconchus* (e.g., *P. macgintyi*) (less than 35 mm length). This genus is gregarious, and may form large (<1 m height) reef structures in some shallow, intertidal waters (Ortiz-Corps 1985).

In the Ten Thousand Islands area of Florida, longshore currents carry sand and shells to areas suitable for oysters to become established. These oyster reefs (Figure 5) then provide stable substrate for mangroves, another important nursery habitat, to take hold (Lodge 1998). In some areas it has been hypothesized that vermetid gastropod reefs provide a similar substrate for mangrove initiation (Davis 1997). Unfortunately, some researchers note that vermetids appear to be in global decline (R. Bieler, Field Museum of Natural History, personal communication).

Although not a vermetid, a common component of the "shellhash" in New England is the slipper limpet (*Crepidula fornicata*), which is a gastropod that often forms dense clusters of mutually adhering individuals and blankets of shell fragments.

B) Aggregations of Living Shellfish

The term "aggregation" is used here to refer to shellfish species that are not attached to one another yet occur at densities sufficient to provide structural habitat for other organisms (Figure 1a- Plate D). The term 'bed' is also sometimes used to refer to the same type of structure. Three groups of bivalves— scallops, pen shells, and *Rangia* —form habitat in this way (Figure 1). Although not molluscan, brachiopods also form dense aggregations that function like other molluscan species.

<u>Scallops</u>

The major habitat-forming scallops that occur along the Atlantic and Gulf coasts are the bay scallop (*Argopecten irradians* with several recognized subspecies) (Figure 1b- Plate B), calico scallop (*Argopecten gibbus*), and sea scallop (*Placopecten magellanicus*) (Bourne 1964; Shumway 1991; Blake and Graves 1995).

Bay scallop (*Argopecten irradians*)

Bay scallops are found on the Atlantic and Gulf coasts from the north shore of Cape Cod, Massachusetts to Laguna Madre, Texas (Waller 1969; Fay et al. 1983). They can reach a maximum size of 60 to 70 mm. Seastars, wading birds, gulls, pinfish, lightning whelks, cow-nosed rays, crabs, starfish, and humans are among the numerous predators of the bay scallop (Peterson et al. 2001a). Scallops are hermaphroditic, with a single individual releasing sperm before eggs (Bricelj et al. 1987). Bay scallops reach sexual maturity within one year, spawning from August through October. The juvenile stage is reached after about 35 days post-fertilization, when they resemble a small adult in shape; their lifespan is less than two years (Peterson et al. 1989).

Bay scallops can migrate en mass. In many areas they have declined significantly (e.g., North Carolina). Red tides, often referred to as "harmful algal blooms," can kill millions of adult and larval bay scallops each year. Scallops grow fastest during the warmer months when food is available. They prefer estuaries and bays where salinities are relatively high, waters are 0.3 to 0.6 m deep at low tide, and seagrasses such as eelgrass (*Zostera marina*) or shoal grass (*Halodule wrightii*) are common (Smith et al. 1988; Prescott 1990; Pohle et al. 1991; Garcia-Esquivel and Bricelj 1993; Bologna and Heck 1999, 2002; Bologna et al. 2001). These grass beds offer protection from predators as well as sites for juvenile attachment (Pohle et al. 1991; Bologna and Heck 1999). In New England waters, the bay scallop habitat is commonly associated with eelgrass beds, due to the attachment value of the vertical blades for early growth and predator avoidance (L. Stewart, University of Connecticut, personal communication).

Bailey (2003) and Lescinsky (1993, 1995) showed that fouling organisms are common on dead *A. irradians* valves on the uppermost interior or exterior portions, supporting the potential habitat value of bay scallop shells where they are common. The epibionts observed included encrusting bryozoans, the bivalve *Anomia simplex*, the slipper shell *Crepidula fornicata,* serpulid polychaete tubes, *Balanus* spp., tubicolous amphipods, hydrozoans, non-calcareous bryozoans, and filamentous red algae (Bailey 2003). For bay scallops, there is a reasonably extensive literature that focuses on its population genetics (e.g., Krause and Bricelj 1995; Wilbur and Gaffney 1997; Seyoum et al. 2003). One North Carolina study showed that a crash in the numbers of bay scallops on one of the most productive beds in the state was in large part do to schools of migrating cownose rays (Peterson et al. 2001b).

Atlantic calico scallop (*Argopecten gibbus*)

The Atlantic calico scallop, a relatively small scallop ranging from 25 to 60 mm shell height, is patchily distributed on the Atlantic coast from Delaware Bay south into the Caribbean Sea to about 20° N latitude. It is most commonly found from just north of Cape Hatteras, North Carolina to the Greater Antilles, and throughout the Gulf of Mexico and Bermuda (Allen and Costello 1972; Blake and Moyer 1991). Genetic and morphological similarities (Waller 1969) between Florida and North Carolina populations and coastal currents support a hypothesis that Florida may be an important larval source for North Carolina stocks (Wells et al. 1964; Krause et al. 1994). Calico scallops can be found in depths of 10 to 400 m, but have been reported from shallower waters in Biscayne Bay (Coleman et al. 1993).

Spawning occurs throughout the year, but peaks in late fall and in the spring (Arnold 1995). As with bay scallops, calicos are simultaneous hermaphrodites that release sperm and eggs. Settling calico scallops require shell or other hard substrate to provide an anchor for byssal attachment. Laboratory studies suggest that after drifting freely for 14–16 days, larvae attach to hard substrates, which are often the disarticulated shells (dead accumulations that are separated or broken) from previous generations (Ambrose and Irlandi 1992; Ambrose et al. 1992). They reach a commercial length of 47 to 53 mm in six to eight months.

The maximum life span of an Atlantic calico scallop appears to be about 24 months. Predation (Wells et al. 1964) is a major factor affecting survival during various phases of the calico scallop life cycle. Aggregations of calico scallops provide habitat for numerous species, including other types of scallops, fish, and invertebrates. Schwartz and Porter (1977) collected 111 species of fish and 60 species of macroinvertebrates, including 25 crustaceans, 12 echinoderms, 4 coelenterates, and 1 annelid. Many of the fish caught used this habitat for feeding purposes (Schwartz and Porter 1977).

Sea scallop (*Placopecten magellanicus*)

Although sea scallops do occur in shallow, nearshore waters, they are more typically found in cooler (< 15^{o}C) offshore waters that are deeper than 40 m (Bourne 1964; Serchuk et al. 1979; Mullen and Moring 1986; Serchuk and Muraski 1997). Sea scallops cannot tolerate temperatures above 22^{o}C, and their optimum is at approximately 10^{o}C (Serchuk and Muraski 1997). These scallops grow rapidly during the first several years of life; water flow and food availability have significant impacts on the ultimate size of the organism (Krantz et al. 1984; Eckman et al. 1989; Claereboudt et al. 1994; Claereboudt and Himmelman 1996; Grant et al. 1997). Between the ages of three and five years, sea scallops increase in size as much as 50% to 80% and quadruple their meat weight. Adults are large, attaining a maximum shell height of about 230 mm.

Sea scallops range from the Gulf of Maine down through the mid-Atlantic approximately to the border between Virginia and North Carolina (Carsen et al. 1995). Adult sea scallops primarily occur on hard bottoms consisting of cobble, gravel, shell and/or sand (Stokesbury 2002); similarly, juvenile habitats include bottoms with cobble, shells, and silt (Carsen et al. 1995).

Predators of sea scallops include sea stars, wolffish, ocean pout, sculpins, American plaice, winter flounder, yellowtail flounder, eelpout, rock crabs and lobster (Elner and Jamieson 1979). Substrate type may affect predation, with increased complexity providing refuge and decreasing predator effectiveness (Jamieson et al. 1982; Barbeau et al. 1994; Nadeau and Cliché 1998). Spawning occurs from May through October, with peaks in May and June in the mid-Atlantic and in September and October on Georges Bank and the Gulf of Maine.

Miller and Buttner (2000) have suggested that a symbiotic relationship exists between red hake (*Urophycis chuss*) and sea scallops. They state that as many as two to four young-of-year red hake can often be found at one time using single scallop shells as shelter.

Pen shells (Pinnidae)

Pen shells are large bivalves that bury partly into the substrate and are anchored by a substantial byssus (long, fine, silky filament). The upper portion of the shell protrudes above the substrate (often referred to as 'emergent shellfish beds'), which provides habitat for other organisms when they occur in sufficient densities (Figure 1a- Plates A & B). Three species of pen shell occur along the Atlantic coast of the Americas: the saw-toothed pen shell (*Atrina serrata*), the amber pen shell (*Pinna carnea*), and the stiff pen shell (*Atrina rigida*) (Abbott 1974).

A. serrata is typically found in sandy mud at depths of up to 6 m. It ranges from North Carolina to Texas and northern South America, and is relatively common in many areas in North Carolina (Abbott 1974). Several recent studies have shown that pen shells are adept at repairing damage in a short time, pointing to potentially interesting resource allocation issues (e.g., cost of shell repair) with regard to this relatively large infaunal organism (T. Alphin, University of North Carolina at Wilmington, personal communication). Many small shrimp and crab species spend their adult lives in the mantle cavity of this species and other pen shells, where they find refuge and feed on particles brought into the mantle cavity (Abbott 1974).

Although *P. carnea* is generally found in sandy areas with depths up to 4 m, it rarely is found in the intertidal zone. It ranges from southeastern Florida to northern South America. Finally, *A. rigida* is common in sandy muds from low intertidal to 27 m in depth. It ranges from North Carolina to southern Florida and the West Indies (Abbott 1974).

As with other filter feeders, pinnids can filter large quantities of suspended sediments and plankton out of the water column, thereby affecting phytoplankton levels and water clarity. However, high densities generate both feces and pseudofeces affecting the surrounding sediments and associated organisms (Cummings et al. 2001; Ellis et al. 2002). For example, Ellis et al. (2002) showed that sedimentation can significantly impact *Atrina* spp. populations.

All three species can occur in large numbers and protrude above the sediment's surface (Figure 1a- Plates A & B). Their shells are typically covered with a diverse assemblage of fouling organisms, including barnacles and slipper shells, which create vertical structure and fish habitat (Kuhlmann 1994, 1996, 1997, 1998; Munguia 2004). Many organisms use the shells as shelter, including crabs (e.g., *Pilumnus sayi*, *Menippe* spp., *Portunus ordwayi*) and benthic fishes such as blennies and gobies) within seagrasses (Kuhlmann 1994). Shells can reach densities of over 13 individuals/m^2 (Kuhlmann 1994, 1996).

Additionally, the Florida blenny (*Chasmodes saburrae*), feather blenny (*Hypsoblennius hentzi*), clingfish (*Gobiesox strumosus*), and Gulf toadfish (*Opsanus beta*) use dead pen shells as nest sites (Kuhlmann 1994). Females lay a single layer of eggs on the inside of the pen shells. Similarly, Joubin's pygmy octopus (*Octopus joubini*) also lays its eggs on the inside of pen shells. Horse conchs (*Pleuroploca gigantea*) are the primary predators of pen shells (Kuhlmann 1994, 1996, 1997, 1998). Dead pen shells provide nesting sites and shelter for many fish species, but are not permanent benthic features. As the shells begin to break apart, the waves and currents sweep them away, thus changing the dynamics of the populations of the species that depend on them (Kuhlmann 1996, 1998).

The most extensive studies of pen shell communities as habitat were completed by researchers in New Zealand (Keough 1984; Cummings et al. 1998, 2001; Nikora et al. 2002; Gibbs et al. 2005). These habitats are also referred to as 'horse mussel' (*Atrina zelandica* and *Atrina novaezelandiae*) beds (Figure 1a- Plates A & B). Research has included fine scale boundary layer flow studies (Nikora et al. 2002), mesoscale hydrodynamic interactions (Green et al. 1998), community interactions (Keough 1984; Cummings et al. 1998, 2001), and essential fish habitat delineation for juvenile finfish species (Morrison and Carbines 2006).

Estuarine wedge clam (*Rangia cuneata*)

The estuarine wedge clam is found in Atlantic coastal and Gulf of Mexico oligohaline estuaries (Cain 1975; LaSalle and de la Cruz 1985; Abadie and Poirrier 2000), tidal rivers, and backwater bays with regular inputs of fresh water. It occurs from the upper Chesapeake Bay to Mexico, often dominating benthic biomass in low salinity areas of estuaries (Cain 1975). This clam is regarded primarily as a subtidal species found in coastal areas with a large tidal range (Estevez 2005).

The species serves as an important link in the food chain, filtering large volumes of water when at high densities and serving as a food source for fish, crabs, and ducks (LaSalle and de la Cruz 1985). In North Carolina, *Rangia cuneata* are often found within the most critical oyster habitat areas where shells accumulate over long time periods. In these areas, accumulations of estuarine wedge clam shells provide substrate for formation of oyster reefs. In a majority of cases, both living and dead *Rangia cuneata* occur together. Estuarine wedge clams are more abundant in downstream reaches and as intertidal material in upstream reaches. Interestingly, live *Rangia cuneata* in intertidal areas can be larger than those in subtidal beds (Estevez 2005).

In Lake Pontchartrain, Louisiana, individual estuarine wedge clams have an average life span of four to five years. Deposits of wedge clam shells in the lake bottom supported a shell mining industry from 1933 to 1990 (Abadie and Poirrier 2000). As with oyster shells, clam shells used to be so abundant that they were used for construction of roadways, parking lots, levees, and in the production of cement. Large (> 20 mm) *Rangia cuneata* were abundant in Lake Pontchartrain in the early 1950s, but became rare by the 1970s and 1980s. They can dominate the benthos, with densities reaching 1,896 clams/m^2 and dry weight biomass as high as 70 g/m^2. However, clams are absent from areas that are subject to anoxia and hypoxia, or saltwater intrusions (Poirrier and Spalding 2005).

Current *Rangia cuneata* studies are seeking to document similar ecological services to oysters, in order to generate interest in its restoration (M. Poirrier, personal communication). Results indicate that increasing clam abundance by decreasing saltwater intrusion will improve water clarity; this in turn should increase submerged aquatic vegetation and add shell for mud stabilization and erosion reduction. These improvements should reduce eutrophication, improve water quality, and enhance fish habitat (M. Poirrier, personal communication).

Carolina marsh clam (*Polymesoda caroliniana*)

This brackish-water corbiculid clam (often reaching sizes over 50 mm, but typically 25-40 mm) is often common in low salinity marshes comprised of plants such as *Juncus* sp. and near river mouths (Andrews and Cook 1951; Andrews 1977; Duobinis-Gray and Hackney 1982; Marelli 1990). The geographical range of this species is from Virginia through Florida along the Gulf of Mexico to Texas, with adult densities often exceeding 300 individuals/m^2 (Duobinis-Gray and Hackney 1982) and juvenile (<20 mm) densities at almost 2,000/m^2 (Marelli 1990). The Carolina marsh clam lives primarily in the intertidal zone (Marelli 1990), but may be found subtidally, in mud to fine sediments (Heard 1982). Some researchers have suggested competitive interactions with another common low salinity bivalve, *Rangia cuneata* (more often subtidal, as *Polymesoda* is a poor burrower in intertidal areas) (Duobinis-Gray and Hackney 1982). Early growth can be rapid (>1 mm/month) (Olsen 1973, 1976), and predation, competition, and inundation are often cited as factors controlling the distribution and abundance of this species (Andrews and Cook 1951, Andrews 1977). A related species *P. maritima*, the Florida marsh clam, is common in the Gulf coast region, and southern Florida to the Yucatan (Andrews 1977).

Little is known about the habitat value of shell accumulations or live aggregations of *Polymesoda* spp. for other organisms.

Brachiopods

Brachiopods, although not molluscs, often form dense aggregations of living and dead shell that are functionally quite similar to molluscan species (Thayer 1979, 1983, 1985; Witman and Cooper 1983). There is anecdotal information that they can be quite abundant in shallow water, for example off the Peninsula Valdez in Argentina, where they form dense terebratulid brachiopod clusters on soft substrata in shallow-water environments (R. Aronson, personal communication). Also, in the New Zealand fjords there are subtidal rocky shore habitats dominated by brachiopods (Witman and Cooper 1983).

C) Shell Accumulations

The shells of dead molluscs sometimes accumulate in sufficient quantities to provide important habitat. The term ‘shell hash’ refers to accumulations consisting mostly of pieces of broken shell (Anderson et al. 1979; Street et al. 2005), although this hash can also be composed of intact small bivalves and gastropod shells (e.g., Sanibel Island, FL). Shell accumulations can occur from estuaries out to the continental slope, with several species present in each zone (Stanley and Dewitt 1983, Stanley 1985, Newell and Hidu 1986, Rice et al. 1989, MacKenzie and McLaughlin 2000, Kraeuter et al. 2003). For accumulations of smaller molluscs, we know little or nothing about their importance (W. Arnold, Florida Fish and Wildlife Research Institute, personal communication).

Accumulations of eastern oyster shells are a common feature in the intertidal zone of many southern estuaries, particularly along waterways impacted by wind and boat wakes (Figure 1a- Plate D) (Anderson et al. 1979; Bahr and Lanier 1981; Grizzle et al. 2002). The dead shells of blue mussels (*Mytilus* spp.) occur intertidally in some northern estuaries. These accumulations, sometimes extending well above the high tide line, have not been well studied. Subtidal shell accumulations, however, provide habitat for many species of commercially and recreationally important fish (Auster et al. 1991, 1995; Holt et al. 1998).

Steimle and Zetlin (2000), Lehnert and Allen (2002), Tolley et al. (2005), and Tolley and Volety (2005) all state that shell can provide many of the same functions as a three-dimensional living reef, although on a slightly smaller scale (Coen and Luckenbach 2000; O’Beirn et al. 2000; Luckenbach et al. 2005). With oyster shell often in short supply, some shellfish restoration projects have even employed alternative materials in lieu of oyster shell (e.g., *Spisula* shell) for initial reef construction (Luckenbach et al. 1999; Coen and Luckenbach 2000; LA DWF 2004). In many ways, early oyster restoration projects involving only placement of shell "cultch" material onto the bottom have the same effect as shell accumulations before large numbers of live oysters recruit and develop on the reef (Powell et al. 2006). Shell accumulations provide more complexity than sandy or mud bottom substrates and can support smaller organisms or early life stages (Steimle and Zetlin 2000; Lehnert and Allen 2002).

Many studies have documented the importance of shell accumulation habitats to fish species (Steimle and Zetlin 2000; Lehnert and Allen 2002; Szedlmayer and Howe 1997; Auster et al. 1991, 1995). For example, Lehnert and Allen (2002) found that dead oyster shell had substantially more fish than either mud or sand. Seabass were 500 times more abundant on shell bottom than on other substrates. Thirty-six finfish species were collected on this habitat type, including sheepshead (*Archosargus probatocephalus)*, rock seabass (*Centropristis philadelphica*), black seabass (*Centropristis striata*), spadefish (*Chaetodipterus faber*), spot (*Leiostomus xanthurus*), grey snapper (*Lutjanus griseus*), lane snapper (*Lutjanus synagris*), black grouper (*Mycterperca bonaci*), gag grouper (*Mycteroptera microlepis)*, and southern hake (*Urophycis floridana*). The majority of individuals caught were under two years of age. This demonstrates the importance of shell accumulations as nursery areas (Lehnert and Allen 2002).

Some species tend to form shell accumulations more often than others. The shells of two bivalve species, ocean quahogs (*Arctica islandica*) and surf clams (*Spisula solidissima*), commonly accumulate in high densities in coastal and shelf waters. These large and long-lived bivalves support important fisheries (see discussion below). There is abundant literature on both of these species (Merrill and Ropes 1969), including: (1) age, sex, and growth (Jones et al. 1978, 1983; Ropes et al. 1984; Walker and Heffernan 1994; Richardson 1988; Cerrato and Keith 1992; Hurley and Walker 1996; Davis et al. 1997; O'Beirn et al. 1997), (2) recruitment (Chintala and Grassle 2001; Powell and Mann 2005), (3) predation (Dietl and Alexander 1997), (4) population status and structure (Kennish and Lutz 1995; Serchuk and Muraski 1997; Ragnarsson and Thórarinsdóttir 2002; Holmes et al. 2003), and (5) fishing impacts (MacKenzie 1982; MacKenzie et al. 1985a; Haskin and Wagner 1986).

Shell accumulations of ocean quahogs and surf clams are important to the juvenile life stages of many finfish species in shelf waters of the Mid-Atlantic Bight (Auster et al. 1991). During a submersible and ROV study, Auster et al. (1991) noted that areas with shell accumulations had the most species per unit area when compared to other habitat types. Young-of-year ocean pout were abundant in these habitats and were observed using the valves of the ocean quahog as shelter. The majority of all the fish species observed around the shell beds were juveniles (Auster et al. 1991).

Szedlmayer and Howe (1997) found that age-0 red snapper were 70-80% more abundant over shell versus sand substrates, possibly because shell provides food or cover for the snapper. Other species show similar associations, including longhorn sculpin (*Myoxocephalus octodecemspinosus*), little skate (*Leucoraja erinacea*), American lobster (*Homarus americanus*), red hake (*Urophycis chuss*), and black sea bass (*Centropristis striata*) (Auster et al. 1991, Auster et al. 1995, and Szedlmayer and Howe 1997).

Humpback whales also feed in areas with shell accumulations. Hain et al. (1995) observed a feeding behavior where whales brush the bottom sediments to feed on sand lances (*Ammodytes dubius*) as they enter the water column. Sand lances spend much of their time burrowed in the substrate, with high densities in shell-dominated bottoms (Collette and Klein-MacPhee 2002).

D) Important Characteristics of the Four Types of Shellfish Habitats

The three major types of shellfish habitat (reefs, aggregations, and accumulations) differ in their combinations of habitat characteristics. However, all shellfish habitats have three major features in common that are the basis for their ecological value for managed species: hard substrate (for settlement/refuge/prey), complex vertical (3-D) structure (for settlement/refuge/prey), and food (feeding sites for larger predators).

Perhaps the most fundamental characteristic of shellfish habitat is hard substrate. The shells provide attachment surfaces for algae and sessile invertebrates, such as polychaetes (e.g., sabellids, serpulids), hydroids, bryozoans, and sponges, which in turn provide substrate for other organisms. Planktonic larvae of some shellfish species, such as oysters, need a hard substrate on which to settle in order to grow into adults (Galtsoff 1964). In many estuarine areas, oyster shell and cultch are the primary settlement material for larval oysters (Kennedy 1996; Powell et al. 2006). All three types of shellfish habitat—reefs, aggregations, and accumulations—provide suitable substrate for other shellfish and many other species that require hard substrate on which to grow.

Sufficient accumulations of hard substrate result in complex habitat structure that provides increased vertical relief and internal complexity of the structure itself. Structural complexity has historically been considered to be an important factor affecting the spatial distribution and diversity of marine and estuarine organisms (Bell et al. 1991). An increase in the physical complexity of an environment is typically correlated with an increase in microhabitat diversity (Sebens 1991). The increase in surface area provides more refuge and feeding sites, which subsequently leads to greater species richness (Bell and Galzin 1984). The interstitial spaces provide recruiting oysters with adequate water flows for growth and refuge from predators, both of which are essential for long-term maintenance of the reef structure (Bartol and Mann 1997; Bartol et al. 1999; Coen et al. 1999b; Powell et al. 2006). Oysters and other reef-forming shellfish can be considered "bioengineers" because they create habitat that allows many additional species to thrive (Jones et al. 1994, 1997).

All four shellfish habitat types provide food for other organisms, whether it is the shellfish themselves or associated organisms. As previously mentioned, oysters and mussels are consumed by many species of fish and invertebrates. Many other species of plants and animals also occur on shell accumulations and provide food for a variety of predators. When considered in combination with the hard substrate and complex structure provided by live shellfish, their direct food value results in shellfish reefs and aggregations being uniquely valuable habitat for many managed species.

E) Ecosystem Services Provided by Shellfish Habitats

The ecological processes that depend on the above characteristics of shellfish habitat can be thought of as "ecosystem services." Hence, in addition to their direct habitat-related value for managed species, shellfish habitats provide important services for the ecosystem as a whole. Three of the most important of these services are discussed in more detail below: refuge, benthic-pelagic coupling, and erosion reduction (or shoreline protection).

Refuge

The term refuge is used here to describe the protective function that shellfish habitat provides for the shellfish themselves, as well as for other organisms that occur in shellfish habitat. This ecosystem service largely results from the increase in structural complexity in shellfish habitat compared to surrounding areas (particularly soft sediments). In other habitats, such as seagrasses or salt marshes, the concept of structural complexity is often associated with the notion of "nursery areas," which refer to places where juvenile invertebrates and fish are protected from predators (Lindberg and Marshall 1984; Heck et al. 1995; Benaka 1999; Halpern et al. 2001; Williams and Heck 2001; Beck et al. 2003; Heck et al. 2003; Minello et al. 2003). Shellfish habitat plays a role similar to seagrasses and other structurally complex habitats in this respect. Most of the research dealing with these topics for shellfish habitat has been done on the reef-forming species, but some information is available for shellfish aggregations and shell accumulations.

Benthic-pelagic coupling

This term refers to the transfer of materials and energy between the bottom community and the water column. It is probably most often used to refer to the overall effect of suspension feeders as they remove suspended particulates from the water column (Dame 1996). The result is a transfer of materials and energy from the water column to the benthos (Frechette et al. 1989; Meyer and Townsend 2000; Cummings et al. 2001; Dame et al. 2001; Ellis et al. 2002).

These feeding activities also typically cause a reduction in turbidity of the water column which has a positive impact on submerged aquatic vegetation (SAV), allowing more light penetration and higher rates of photosynthesis (Meyer and Townsend 2000). The shellfish release ammonia and other metabolites that are nutrients for the SAV. Therefore, SAV (Peterson and Heck 1999, 2001a, 2001b; Williams and Heck 2001; Heck and Orth 2006) and oyster reefs potentially play mutually beneficial roles (Heck 1987; Newell 1988; Dame 1996; Dame et al. 2001; Newell and Koch 2004) (also see Pomeroy et al. 2006 for a different perspective).

Oyster reefs are likely to reduce eutrophication by mediating water column phytoplankton dynamics and denitrification (Dame 1996; Newell et al. 2002; Newell 2004). A decrease in oysters in the Chesapeake Bay has led to increased phytoplankton numbers and reduced competition with zooplankton. An increase in zooplankton leads to a rise in predators, such as ctenophores and jellyfish. An increase in phytoplankton also leads to a microbial shift and anoxic conditions of deeper waters in areas such as the Chesapeake Bay (Ulanowicz and Tuttle 1992; Newell 1988) (also see Pomeroy et al. 2006 for another view). Models have shown that an increase in oyster abundance would reduce phytoplankton primary productivity and secondary gelatinous consumers (e.g., ctenophores) to historically low levels (Ulanowicz and Tuttle 1992).

Erosion reduction

Estuaries in many areas are threatened by increased coastal population growth and associated industrial, residential, and recreational development and utilization (Vernberg et al. 1999). One major area of recreational growth has been in the number of people with Class A (< 16 ft) and Class 1 (16 to 25 feet) motorized boats utilizing these waterways (NMMA 2004).

Some problems related to this increase in the number of small boats have been well documented (Crawford et al. 1998; Cyr 1998; Backhurst and Cole 2000; Bauer et al. 2002; Kennish 2002). For example, increases in seagrass scarring from boat propellers and the number of marine mammal collisions are both positively correlated with increased boating activity (R. Virnstein, personal communication; Sargent et al. 1995).

However, little is known about the direct and indirect impacts of boating on other critical estuarine habitats in the landscape, such as intertidal oyster reefs (Grizzle et al. 2002; Coen and Fisher 2002; Coen and Bolton-Warberg 2003, 2005; Piazza et al. 2005; Wall et al. 2005). Those areas dominated by intertidal oyster reefs form a protective breakwater for fringing *Spartina* marshes, retarding shoreline erosion (Coen and Fischer 2002; Coen and Bolton-Warberg 2005).

Additionally, shoreline erosion in tidal channels is an issue in many states (Cyr 1998; Gabet 1998). Undercutting by wind waves and boat impacts can cause slumping (calving) of large masses of sediment embedded with *Spartina* (Gabet 1998; Chose 1999; Piazza et al. 2005). *Spartina* has been documented to be an important habitat for estuarine productivity (e.g., as a feeding ground for juvenile fishes and their prey) and is known to perform many other ecological functions, such as buffering run-off (Weinstein and Kreeger 2000).

Data collected by researchers from the South Carolina Department of Natural Resources noted significant shoreline losses at numerous study sites (n = 11) across South Carolina (Coen and Bolton-Warberg 2005). By reducing erosion, oyster reefs reduce vegetation loss and preserve other habitat types (Meyer and Townsend 2000). They also stabilize creek banks and help to reduce erosion of marshes (Meyer et al. 1997; Chose 1999; Coen and Fischer 2002; Breitburg et al. 2000; Coen and Bolton-Warberg 2003, 2005; Piazza et al. 2005), but may be easily impacted by boat wake or storm damage (Grizzle et al. 2002; Coen and Bolton-Warberg 2005).

Research on recreational boating impacts on estuarine species is surprisingly still in its infancy (Anderson 1976, 2000; Kennish 2002; Bishop 2003, 2004, 2007; Bishop and Chapman 2004). Productivity, diversity, and survival of estuaries in the southeastern United States are threatened by explosive coastal population growth and associated industrial, residential and recreational development and utilization (Vernberg et al. 1999). In spite of the potentially far excursion distances of motorboats, and the large number of boats on the water on any given day, sparse data exist to quantitatively determine the impact of boat wakes on intertidal organisms.

In conclusion, it should be noted that each of the four types of shellfish habitats differ with respect to their major characteristics and the ecosystem services they provide. Shellfish reefs typically provide the most in the way of services because they consist largely of live animals that provide a food source for many fish and invertebrates, and typically have significant vertical structure. Shellfish aggregations consist mainly of live animals but typically do not occur at densities as high, or with vertical structure as extensive, as shellfish reefs. Shellfish accumulations consist only of the dead shell remains, but they provide hard substrate and may have significant vertical structure. There is a rich literature that documents the importance of all four types of shellfish habitat to many species of fish and invertebrates, including most species managed by the ASMFC.

III. STATUS OF HABITAT-CREATING SHELLFISH SPECIES

Throughout history, bivalves have been harvested as a human food source. Shell middens from native Americans have been found throughout the Atlantic coast of North America, often with oyster shells that are much larger than living shells found today (Brooks 1891; Churchill 1920; Kennedy and Sanford 1999). The middens primarily consisted of eastern oysters, but also hard clams, blue and ribbed mussels, and slipper snails (Mackenzie and Burrell 1997). The middens show that Native Americans consumed and traded bivalves extensively, and they were used in a variety of ways, including as ornamentation, scrapers, spoons, knives, fish hooks, and money (Kent 1992; Burrell 2003).

The harvest of molluscs by European settlers (Dutch, English, and French colonists) first began in North America in the 1600s. In colonial days, mid-Atlantic mollusc stocks were abundant. However, most species that supported commercial fisheries were seriously depleted over the ensuing centuries (MacKenzie 1996, 1997; Mackenzie et al. 1997a, 1997b, 1997c). A recent review chronicles the history of shellfish depletion in North America as harvesters dispersed among major cities north and south of the mid-Atlantic region where the earliest harvesting by European settlers occurred (Kirby 2004).

Between 1900 and 1902, bivalve landings totaled about 164 million pounds of meat, including 143 million pounds of oysters, 10 million pounds of hard clams, 10 million pounds of softshell clams, and 1 million pounds of bay scallops. Surfclams and ocean quahogs were not fished at this time. By 1991, oyster landings had been reduced by 85%, northern quahog landings remained stable, and softshell clams and bay scallops had been reduced by 40% (MacKenzie and Burrell 1997; Mahmoudi et al. 2005). The dramatic declines in oyster harvest reflect extensive losses of shellfish habitat in nearly all estuaries in the mid-Atlantic and northeastern states. Shellfish habitat losses associated with other harvested species such as mussels and scallops vary, but none have been so severely affected as oysters.

Oyster status

Oysters were once abundant in nearly all the estuaries on the Atlantic and Gulf coasts of the United States (MacKenzie and Burrell 1997). Oyster reefs once grew so extensively that they were considered to be a navigational hazard (Brooks 1891; Newell 1988; Rothschild et al. 1994; Luckenbach et al. 1999; NRC 2004; Kirby 2004). It was also reported that in the 17th and 18th centuries, oysters were so large that they needed to be divided into two or three portions before they could be eaten (Ingersoll 1881; Wharton 1954).

Today, most oyster stocks have been greatly depleted. Oyster fisheries in Chesapeake Bay, Delaware Bay, and Pamlico Sound have been decimated. In the 1800s, the Chesapeake Bay produced approximately 20 million bushels of oysters per year. By the early 1990s, Chesapeake Bay oyster landings totaled only 123, 618 bushels (MacKenzie 1997). Landings of the eastern oyster have decreased by over 90%, and over 50% of oyster habitat has disappeared from the Chesapeake Bay (Kirby 2004; NRC 2004). As a result, oyster fisheries in North Carolina and in the Chesapeake and Delaware Bays are well below historical highs (Rothschild et al. 1994; Kirby 2004; NRC 2004).

From the late 1800’s to the 1950’s, oyster reefs in Connecticut and New York covered thousands of acres and produced 2 to 3 million bushels of oyster per year (Korringa 1976).

Subsequently, natural oyster production declined for three decades, until the innovative use of large qualtitities of cultch was implemented (e.g., Powell et al. 2006). The cultch was placed in July for natural spat set, which resulted in increased seed oysters for transplant to New York, Rhode Island, and Massachusetts (Kochiss 1974). The practice of artificial cultch placement enhanced the acreage of shell habitat dramatically. For example, Connecticut production involved over 45,000 acres of franchised beds, and in the early 1990's produced more than 1,000,000 bushels of oyster (L. Stewart, University of Connecticut, personal communication).

The shell substrate habitat created by the cultivation process is a put-and-take operation, causing dramatic changes to seabed characteristics. The sequence of the use of cultch proceeds as follows: (1) collection of dried cultch (including oyster, clam, and/or scallop shell), (2) placement on private seabed leases or designated public natural shellfish grounds, (3) transplant of spat seed to grow out beds in deeper water, and (4) the final harvest and transfer to market (Volk 1986b). Oyster ground maps (i.e., Milford, CT) indicate the extensive use of Connecticut coastal waters for oyster/clam production and shell substrate management (Volk 1986a). Connecticut state bond appropriations ($1,000,000 per year) contributed to exponential industry growth in the 1990's; the cooperation of industry, state appropriations, and towns resulted in "shelling" tens of thousands of acres of bottom in the Long Island Sound (L. Stewart, University of Connecticut, personal communication).

The overall decline in oyster harvest and the associated destruction of oyster reefs along the Atlantic coast has been caused by many factors, including overfishing, habitat destruction, shortages of hard substrate for spat settlement, reduced water and habitat quality, natural and introduced predators, and diseases (MacKenzie and Burrell 1997; Coen et al. 1999a, 1999b; MacKenzie 1996). There is a fast-growing body of literature on the issue of oyster decline; the focus here is on restoration programs because many restoration efforts deal explicitly with ecological functions of the oyster, instead of, or in addition to, the traditional focus of managing a human food resource.

Probably the most widely used technique for restoration of eastern oyster populations has been the placement of shell or other "cultch" material directly onto existing oyster bottom (or areas of potential oyster habitat) to provide suitable substrate for natural settlement of spat (Soniat et al. 1991; Haywood and Soniat 1992; Luckenbach et al. 1999; Soniat and Burton 2005; Powell et al. 2006). This well tested restoration technique has been shown to be effective as well as relatively inexpensive (Haven et al. 1978; Kennedy 1989; Hargis and Haven 1999; Kennedy and Sanford 1999). But its effectiveness depends on a number of factors, including the kind of cultch material used, placement of the cultch, and environmental conditions (e.g., siltation rates, prevalence of disease, and reproductive output of the native oyster populations). For example, in the Chesapeake Bay region, extensive shell planting programs resulted in substantial increases in oyster production from the 1940s until oyster diseases became widespread (MacKenzie 1996). For the past several decades oyster populations have continued to decline; as a result, researchers are testing a variety of restoration methods that can be used in conjunction with shell plantings (Luckenbach et al. 1999; Coen and Luckenbach 2000).

In fact, since initiating a highly successful pilot project in 2003, New Jersey has employed a multiphase enhancement process in Delaware Bay, taking advantage of environmental differences throughout the Bay that affect recruitment, growth, and survivorship. Cultch is planted in areas of the lower Bay with historically high oyster set (but high disease and predation mortality). After oysters have set on the planted shell, the spatted shell is reharvested and transported to the central part of the Bay where favorable conditions limit disease and predation mortality, but growth is adequate such that many oysters reach market size before disease losses become excessive. This process benefits the oyster fishery while providing the habitat benefits important to a variety of estuarine species (J. Joseph, New Jersey Bureau of Shellfisheries, personal communication).

Two diseases have had a major impact on Atlantic oyster populations since the mid-1950s. The vectors of the diseases are the protozoan parasites *Perkinsus marinus* and *Haplosporidium nelsoni,* which have caused significant mortality throughout the species' geographic range (Rothschild et al. 1994; Barber et al. 1997). *P. marinus* causes the disease Dermo and is found in oysters from Maine to Mexico. *H. nelsoni* causes the disease MSX and is found in oysters from Maine to Florida (Coen et al. 1999a). Therefore, most ongoing restoration programs must deal with one or more oyster diseases. Consequently, the most common technique used in conjunction with shell (cultch) plantings is "spat seeding," which uses remotely set larvae from disease-resistant and/or fast-growth broodstock (Castagna et al. 1996; Supan et al. 1999). This approach has the unique dual potential of providing direct population enhancement, in addition to the introduction of disease-resistance and/or fast-growth potential to the local gene pool. Moreover, although each particular operation is different, the remote setting process in general has been found to be a relatively low-cost method for producing seed oysters (Supan et al. 1999).

Oyster restoration programs across the nation are increasingly demanding more shell for planting and remote setting (Putnam 1995; Brumbaugh 2000a, 2000b; Coen and Luckenbach 2000; Henderson and O'Neil 2003; LA DWF 2004). The decline of oyster landings (and subsequently shucked shell) in many areas traditionally known for significant oyster harvests has increased the pressure on subtidal deposits of fossil shell (3,000 to 4,000 years old) to meet restoration goals. This need could ultimately impact other near-surface shell accumulations ripe for harvesting offshore. In Maryland alone, dredging to reclaim buried shell deposits often amounts to 2 to 3 million bushels/year, in addition to Maryland's past multi-million bushel harvests. Alternative or new sites for shell mining (Henderson and O'Neil 2003) are potentially available, but many fall within fishery management zones that are seasonally important as spawning or nursery grounds for anadromous and other economically important fish species.

Many Gulf of Mexico states had typically used oyster shell or *Rangia* clam shell, mined from fossil material or deposits in Louisiana, as cultch material for re-building oyster bottoms (Putnam 1995; LA DWF 2004). However, in 1990 a ban was placed on clam shell dredging in Lake Pontchartrain, Louisiana causing a shift in focus to other materials (Leard et al. 1999; Abadie and Poirrier 2000; LA DWF 2004). Recent trials in Louisiana have had excellent restoration success with concrete and limestone relative to oyster shell (LA DWF 2004). However, in the experimental trials, oyster shell was crushed to a smaller size to coincide with the size ranges of #57 concrete and limestone. This potentially may have decreased the value of intact shell cultch versus the other two substrates (LA DWF 2004).

There is concern over depletion of the shell resource itself as well as the environmental impacts of dredging. In addition to offshore clam shell, crushed limestone (or marl) is being studied for use in Florida (M. Berrigan, Bureau of Aquaculture Development, personal communication) and Louisiana (LA DWF 2004); fly-ash, another oyster cultch alternative, has been difficult to procure in recent years (Soniat et al. 1991; Haywood and Soniat 1992; Luckenbach et al. 1999; Coen and Luckenbach 2000; Henderson and O'Neil 2003; M.

Luckenbach, Virginia Institute of Marine Science, personal communication). The North Carolina Division of Marine Fisheries currently uses class B riprap stone from nearby mines to restore oyster reefs in Pamlico Sound. Other states (e.g., Virginia) have tried this material as well as other marl 'relatives' to varied restoration success (LA DWF 2004).

Material density is critical, especially in areas where soft sediments can 'swallow' denser materials. Currently, North Carolina is conducting a side-by-side comparison of marl versus oyster shell on an intertidal site. Preliminary results show poor spatfall on the marl (M. Marshall, North Carolina Division of Marine Fisheries, personal communication). North Carolina has not used marl in the past intertidally, but managers are envisioning future trials, as it is getting more difficult to obtain oyster shell. North Carolina has also used calico scallop (*Argopecten gibbus*) shell and surf clam (*Spisula solidissima*) shell extensively in the past, but those are now also in short supply (M. Marshall, North Carolina Division of Marine Fisheries, personal communication). Calico scallops were used successfully in North Carolina on intertidal sites in the past. However, the supply of these shellfish became scarce once shucking operations moved to Florida years ago (M. Marshall, North Carolina Division of Marine Fisheries, personal communication).

In New Jersey in 2006, the Bureau of Shellfisheries elected to plant approximately 300,000 bushels of shell (20-25% surf clam and 75-80% ocean quahog; no oyster available). They determined this to be a satisfactory substrate for spat settlement following an earlier study that indicated no significant difference in spat settlement between oyster shell and surf clam shell and no significant difference between surf clam and ocean quahog shell. However, there was a significant difference in spat settlement between oyster shell and ocean quahog shell. In light of the scarcity of oyster shell, managers determined that surf clam and ocean quahog were adequate substitutes (J. Joseph, New Jersey Bureau of Shellfisheries, personal communication).

In conclusion, the eastern oyster has suffered dramatic population declines in most Atlantic coast estuaries over the past two centuries. As a result of these declines and the widespread recognition of the ecological importance of oysters, restoration programs that typically address both ecological and human harvest goals are ongoing throughout the range of the eastern oyster. The major implication for managed species is that significant efforts already are underway to enhance the habitat value of bottoms historically dominated by oysters, and in many cases they include construction and/or restoration of reefs with complex vertical structure and other ecologically important attributes. Additionally, it is pertinent to note that as more states recycle fresh shell from shucking houses and other sources, care must be taken not to inadvertently introduce non-natives or other disease strains (Bushek et al. 2004).

<u>Mussel status</u>

Until the late 1970s, mussels had little commercial value in North America (Lutz 1977). Throughout the 1980s, a *Mytilus* aquaculture industry (mainly using bottom culture techniques) developed in New England, with most production occurring in Maine (Lutz et al. 1991; Newell and Shumway 1993; Campbell and Newell 1998; Newell et al. 1998). Since the early 1990s, aquaculture has expanded in the region and now includes suspension-culture techniques including rafts and open ocean longlines (Wallace 1997; Chambers et al. 2003). No mussels other than *Mytilus* spp. support fisheries or aquaculture industries along the Atlantic and Gulf coasts. Mussel landings in the U.S. Atlantic have fluctuated due to changes in the aquaculture industry, because all commercial landings come from bottom or suspension-culture production. We are not aware of any data on abundance trends for natural populations of the blue mussel, nor are we aware of any data that suggest declines in this species. Bologna et al. (2005) have recently examined interactions between the seagrass *Zostera* and episodic recruitment events in *Mytilus* populations.

Scallop status

The status of scallop fisheries depends strongly on the population trends of individual species. Total annual landings of calico scallops have been highly variable due to extreme fluctuations in recruitment success, population size, and changes in market demand. The calico scallop fishery originally developed in North Carolina in the early 1960s. However, the focus of the fishery shifted to the Cape Canaveral, Florida, during the early 1970s, as the extent of those beds was realized and the equipment necessary for large-scale processing was developed (Cummins 1971). Peak landings from the fishery were recorded during the early 1980s, but landings have never again reached even 50% of the 1984 zenith. Calico scallops are now infrequently landed along the gulf coast of Florida except in “boom” years (e.g., 1994, 1998, 1999).

Successful calico scallop recruitment is highly variable (W. Arnold, Florida Fish and Wildlife Research Institute, personal communication). One factor likely influencing year-class success is coastal upwelling, which drives nutrient rich water onto the middle shelf and may aid in retaining larvae over favorable habitat. Some anecdotal reports suggest that intense fishing pressure has removed the ‘shell beds’ necessary for successful scallop recruitment, thus reducing or eliminating future landings (SAFMC 1998a).

It should be noted that successful settlement does not, however, ensure survival to adulthood. Diseases such as *Marteilia* sp. (Moyer et al. 1993) have also triggered significant declines, potentially causing mass mortalities (nearly 100%) off Florida. South Atlantic stock conditions are unknown due to the large fluctuations in calico scallop abundance (SAFMC and GMFMC 1981).

Sea scallops support major fisheries in the mid-Atlantic and northeastern states (Caddy 1989; Shumway 1991). Historically, landings fluctuated widely, and some large geographic areas in the mid-Atlantic and on Georges Bank experienced moratoriums in the 1990s as part of an effort to rebuild depleted groundfish stocks (Muraski et al. 2000). In recent years, standing stocks have increased in both closed and open areas (Stokesbury et al. 2004).

A report by the National Marine Fisheries Service (2002) states that the Atlantic sea scallop fishery has been rebuilt since 1997, and sea scallops off Georges Bank are neither overfished nor approaching an overfished condition. However, in the mid-Atlantic, although overfishing of sea scallops is occurring, they are not considered to be overfished. The National Marine Fisheries Service (2002) describes overfishing as both the harvest rate and stock size being above the prescribed thresholds established in the fishery management plan. There is also an extensive literature from aquaculture-directed studies (Parsons and Dadswell 1992; Beninger et al. 1997; Pilditch 1997; Pearce et al. 1998, 2004; Pilditch et al. 2001).

Surf clam and ocean quahog status

While the surf clam commercial fishery began in earnest in the 1940s, the ocean quahog fishery was initiated approximately 30 years later. These two fisheries are largely conducted with similar vessels equipped with hydraulic clam dredges. Both surf clams and ocean quahog are not in an overfished status, nor are they approaching an overfished condition in most areas (NMFS 2002; Powell and Mann 2005). However, it should be noted that surf clam stocks in the mid-Atlantic region have declined dramatically over the last 10 years. In New Jersey territorial waters, for example, the standing stock of surf clams declined by nearly 86% between 1997 and 2006. Moreover, despite these stock declines, which cannot be accounted for by landings data, surf clam shell has been conspicuously absent from the more than 330 station locations sampled each year in New Jersey waters. In addition, the lack of surf clams as well as the shell may be having negative impacts to the nearshore environment (J. Joseph, New Jersey Bureau of Shellfisheries, personal communication).

Production of ocean quahog is highest in bays from Massachusetts through New York, but the species ranges south to North Carolina. This fishery has historically yielded consistent production (MacKenzie and Burrell 1997). For the past two decades, ocean quahog landings have shifted further north along the Atlantic coastline with substantial landings from southern New England waters (Anderson et al. 1999). An intensive study of population structure on Georges Bank suggested that there has been increased recruitment since 1990 (Lewis et al. 2001). It appears that water temperature changes may indeed be affecting the ranges of these offshore species (E. Powell and R. Mann, South Carolina Department of Natural Resources, personal observation).

Surf clam, ocean quahog, and sea scallop fisheries off the northeastern coast are among the most valuable in the world. In 1993, landings of these three species combined totaled 65,200 metric tons (Serchuk and Muraski 1997).

Currently, other habitat-creating shellfish species do not appear to be under any obvious fishing pressure (Wallace 1997; NMFS 2002), although pen shells and other fragile or patchily distributed molluscan species (e.g., vermetids) are thought to be declining (W. Arnold, Florida Fish and Wildlife Research Institute, personal communication; C. Peterson, University of North Carolina at Chapel Hill, personal communication).

IV. SHELLFISH HABITATS AND ASMFC-MANAGED SPECIES

In this section we present a species-by-species discussion of any known relationships between ASMFC managed species and shellfish habitats. Information on the biology and general ecology of each species is provided, mainly in reference to shellfish habitat.

Table 1 summarizes the information in this section, and identifies the fact that one or more life stages of each of the 22 ASMFC-managed species, or species groups, utilize shellfish habitat at some point in their life histories. Both literature and anecdotal information are included.

Table 2 is a revised version of a table originally found in Coen et al. (1999b), which summarizes the mobile finfish and invertebrates qualitatively and quantitatively collected by various methods on intertidal and/or subtidal oyster reefs from Maryland to Florida. Species in Table 2 that are also ASMFC-managed species are noted with an asterisk (*). Based on recent sampling in and around oyster habitats, Coen et al. 1999b present data on 15 of the 22 (69%) managed species (Table 2). Species missing include the American lobster, Atlantic Sturgeon, horseshoe crab, northern shrimp, scup, spiny dogfish, and *Alosa* spp. A more intensive search may yield additional (non-anecdotal) information for these species on shellfish habitats other than oyster reefs. The focus for these studies of transient finfish and decapods has been from Virginia to Louisiana, with little or no collections north of Virginia and in Georgia.

American eel (*Anguilla rostrata*)

The American eel has been found to associate with oyster reef habitats. Harding and Mann (1999a) listed the American eel as a resident species of an oyster reef in the Piankatank River, Virginia, indicating that all life stages were caught on the reef. Lenihan et al. (2001), Harding and Mann (1999), and Coen et al. (1999a) also observed juvenile and adult American eels near oyster reefs. Coen et al. (1999b) collected American eel around intertidal oyster reefs in South Carolina. They have also been collected on reefs in Maryland, Virginia, and North Carolina (Table 2). This presence of American eels on oyster reefs is likely because they are omnivorous, consuming a wide variety of food items, including bivalve molluscs (Wenner and Musick 1975).

American lobster (*Homarus americanus*)

Lobsters occur in reefs, aggregations, and accumulations of shellfish. They consume molluscs, such as blue mussels and sea scallops, as well as a wide variety of invertebrates including crabs, polychaetes, sea urchins, and sea stars that occur within shellfish habitat (Ennis 1973; Weiss 1970; Elner and Jaimeson 1979). Based on an examination of 288 lobster stomachs in Bonavista Bay, Newfoundland, molluscs (sea scallop, clams, chiton, limpet, and mussels) composed 10.9% of the lobster diet (Ennis 1973). Lobsters also feed on rock crabs that are commonly found on oyster reefs (Newell 1989). Able et al. (1988) and Barshaw et al. (1994) noted the value of salt marsh peat substrates as protection for postlarval lobsters. Additionally, ribbed mussels often occur in high numbers in these areas (L. Coen, personal observation).

Lobsters are often found in shell accumulations (Stewart 1972; Elner and Jamieson 1979; Auster et al. 1991; Auster et al. 1995). In ROV studies of Long Island Sound, juvenile American lobsters were associated with mussel accumulations (Auster et al. 1995); in the mid-Atlantic Bight they were found in shell accumulations consisting mainly of ocean quahog shells (Auster et al. 1991). In their study, Auster et al. (1991) found juvenile lobsters mostly in depressions excavated through dense shell cover. This excavating behavior is thought to be the result of the lobster searching for live shells for food, or creating a daytime shelter (Auster et al. 1995).

Atlantic croaker (*Micropogonias undulatus*)

The Atlantic croaker (also known as drum, golden croaker, or hardhead) occurs on oyster reefs and scallop aggregations. As with other sciaenids such as spot, black drum, and red drum, Atlantic croaker consume oysters and oyster spat (NC DMF 2001). Research in several geographic areas has documented the occurrence of Atlantic croaker on oyster reefs (Harding and Mann 1999; Lenihan et al. 2001; Coen et al. 1999b). Schwartz and Porter (1977) collected Atlantic croaker over a calico scallop aggregation in the ocean off the coast of North Carolina.

Atlantic herring (*Clupea harengus*)

Atlantic herring have been collected in and around oyster reefs in Virginia (Table 2). Shell accumulations are potentially important to the reproductive cycle of herring because they deposit their eggs on a variety of substrates, including boulders, rocks, gravel, macrophytes, and shell fragments (Reid et al. 1999; Munroe 2002). Messieh (1988) observed spawning behavior and reported that herring choose shell, gravel, or bedrock substrate for egg deposition. Otherwise, little is known about the relationship between shellfish habitat and Atlantic herring.

Atlantic menhaden (*Brevoortia tyrannus*)

The Atlantic menhaden is a pelagic species, with all stages of its life cycle mainly occurring in the water column (Munroe 2002). Limited research has been done that directly links menhaden to shellfish bed habitat. However, a number of studies show that menhaden are frequently caught around oyster reefs (Table 2) (Mann and Harding 1998; Lenihan et al. 2001; Coen et al. 1999b). Atlantic menhaden has been collected in and around oyster reef habitats in Maryland, Virginia, North Carolina and South Carolina. Arve (1960) found that an increase in oyster shells was related to an increase in the number of menhaden caught around the reefs.

Atlantic sturgeon (*Acipenser oxyrinchus*)

Atlantic sturgeon are demersal for most of their life cycle; they produce adhesive eggs that stick to hard substrates, such as shell (Dean 1894; Smith and Clugston 1997). Collins et al. (2000) found that adult sturgeon in the Edisto River, South Carolina, use a variety of different substrates during the summer, including mud, sand, pebbles, and shell hash. The lack of hard substrate for the attachment of eggs is considered to possibly be the most limiting habitat requirement of sturgeon in the Chesapeake Bay system (NMFS 1998). Atlantic sturgeon also consume shellfish (particularly mussels), as well as worms, shrimp, and small bottom dwelling fish (Gilbert 1989).

Black sea bass (*Centropristis striata*)

Black sea bass are associated with structural habitats and are considered to be reef fish. Some of the structural habitats that they utilize include oyster reefs, mussel reefs, calico scallop aggregations, rocky areas, shipwrecks, and artificial reefs. Shellfish habitats play an especially important role for the juvenile and young-of-year black sea bass (Lehnert 2000; Lehnert and Allen 2002). Their preferred nursery habitat is a shallow hard bottom with structure that provides refuge. Juvenile fish have often been observed in small groups near artificial reefs or in depressions containing shell fragments in the surrounding sand. In estuaries, they have been found on oyster reefs with summer flounder, spot, bay anchovy, red drum, oyster toadfish, and other species (Table 2) (Smith 1981; Wenner 1992; Wenner and Archambault 1996, 2005).

Young-of-year fish are highly territorial and have been observed defending shells that they use as shelter (Steimle et al. 1999). Some juvenile fish may spend the warmer months along the coast in accumulations of surf clam and ocean quahog shells. Young-of-year black sea bass are frequently collected over shell accumulations, and they have been observed using surf clam valves as refuge (Able et al. 1995; Able and Fahay 1998). Video records and visual observations show black sea bass using surf clam valves during the day at depths of 14 to 20 meters (Able et al. 1995). This shellfish habitat provides quality foraging ground for the young fish, with juveniles feeding on small benthic crustaceans like isopods, amphipods, copepods, small crabs, and small shrimp found in abundance on the beds (Steimle et al. 1999).

Adult black sea bass are found in deeper waters associated with structural habitats including oyster and mussel reefs (Steimle et al. 1999). An experiment by Arve (1960) demonstrated that planting of oyster shells in Chincoteague Bay, Maryland, increased the number of black sea bass caught in that area. Black sea bass were caught on calico scallop aggregations in the ocean off North Carolina year-round. Schwartz and Porter (1977) stated that black sea bass were one of the dominant fish species caught in this habitat.

Sea bass also feed on shellfish. Schwartz and Porter (1977) documented calico scallops in the stomach and intestine of black sea bass and list them as scallop predators. Both juvenile and adult fish had parts of, or whole, scallops in their stomachs (Schwartz and Porter 1977). Black sea bass have been collected in and around oyster reef habitats (Table 2) in Maryland, Virginia, and North Carolina.

Bluefish (*Pomatomus saltatrix*)

The bluefish is a pelagic species, with all life history stages mainly residing in the water column (Klein-MacPhee 2002). However, they are associated with all types of shellfish habitats. Young-of-year are assumed to be estuarine-dependent (Able et al. 2003). Harding and Mann (2001) found more bluefish on oyster reefs than at non-reef sites, and the reefs provided habitat for the fish species that bluefish prey upon. Twenty-five bluefish prey species are found on oyster reefs, including spot, bay anchovy, and Atlantic menhaden. Because bluefish growth rates tend to be higher when their diet includes fish (Juanes and Conover 1994), it is important that these prey species are available to supplement a diet of crustaceans. In addition, increased prey on the reefs may increase both the survivorship and recruitment rates of the bluefish (Harding and Mann 2001a).

Oyster reefs also provide juvenile bluefish with important sources of secondary food resources when there is low pelagic food availability (Able et al. 2003). Bluefish also feed on sand lances, which are commonly found in shell accumulations (Hain et al. 1995). Additionally, Mann and Harding (1998) indicate that gobies and blennies are among the bluefish's major foods. Bluefish have been collected around oyster reef habitats in Maryland, Virginia, North Carolina, South Carolina, Louisiana and Texas (Table 2). Schwartz and Porter (1977) also linked bluefish to calico scallop aggregations.

Horseshoe crab (*Limulus polyphemus*)

Horseshoe crabs are a demersal species associated with the seabed in all life history stages. Shellfish habitats provide horseshoe crabs with an abundant food source. They commonly consume juvenile *Mya arenaria* (softshell clams), *Mercenaria mercenaria* (hardshell clams), and *Gemma gemma* (amethyst gem clams). Botton and Ropes (1989) found that bivalves made up 87% of the total number of food items in the horseshoe crab's diet; most abundant were the surf clam, nut clam, dwarf tellin, and razor clam. Botton and Haskin (1984) noted that 150 horseshoe crabs from a single clam dredge haul off southern New Jersey had been preying on large amounts of blue mussels.

Horseshoe crabs occur all along the U.S. Atlantic coast, with each major estuary having a population that can be distinguished by adult size, carapace color, and eye pigmentation. Delaware Bay is probably home to the largest population of Atlantic horseshoe crabs (Botton and Ropes 1987a, 1987b). Spawning adults prefer sandy beach areas within bays and coves that are protected from wave energy. O'Connell et al. (2003), used stable isotopes to conclude that horseshoe crabs are generalist predators that exhibit a great deal of within-estuary site fidelity in foraging habits. The horseshoe crabs beach habitats should have porous, well-oxygenated sediments to provide a suitable environment for egg survival and development. Differences between coarse- and fine-grained sand, as well as how rapidly the sand drains, affect nest-site selection and nesting synchrony. Preferred egg deposition sites are often next to large intertidal sand flat areas, which provide protection from wave energy and an abundance of food for juveniles. Juveniles usually spend their first two years on these intertidal sand flats.

At least 11 species of migratory birds use horseshoe crab eggs as their primary food supply during their migrations. Therefore these migratory birds can also be found in major estuaries, such as Delaware Bay. The horseshoe crab eggs replenish the fat supply of the migratory birds during their trip from South American wintering areas to Arctic breeding grounds. During the migration, migratory shorebirds can gain as much as 40% or more of their weight from feeding on horseshoe crab eggs (Myers 1986).

Northern shrimp (*Pandalus borealis*)

Little is known concerning the relationship between northern shrimp and shellfish habitats. The only reported association with a particular benthic habitat type is with muds of high organic content (Haynes and Wigley 1969; Shumway et al. 1985). Northern shrimp are important prey for many species such as Atlantic cod, Greenland halibut, skates, wolffish, snow crab and harp seals (CDFO 2004). The Gulf of Maine is the southern extent of the range of *P. borealis,* but it supports a valuable commercial fishery in this region (Anderson et al. 1999).

Red drum (*Sciaenops ocellatus*)

Shellfish habitat is important to red drum. Adults are commonly found feeding on, and around, oyster reef structures (SAFMC 1998b). Their inshore habitats include both oyster reefs and shell accumulations, along with tidal freshwater habitats, low-salinity reaches of estuaries, estuarine emergent vegetated wetlands, estuarine shrub, SAV, and unconsolidated bottom (ASMFC 2002; SAFMC 1998b). Shallow bay bottoms or oyster reefs are listed in the SAFMC's final habitat plan to be the habitat preferred by adults and subadult red drum (SAFMC 1998b). The ASMFC lists oyster reefs and shell beds as Habitat Areas of Particular Concern (HAPCs) for red drum (ASMFC 2002).

Oyster reefs are particularly important habitat for the juvenile (year 1) red drum in some geographic areas (Wenner 1992). Seagrass beds are the primary habitat of juvenile red drum in some states; however, in states where little or no SAV exists, shellfish bed habitat becomes the primary habitat. This is the case in South Carolina and Georgia. In South Carolina, juveniles move from shallow marsh areas to deeper waters during the fall months. In the deeper estuarine areas, they are associated with river mouths, oyster reefs, and beaches (Daniel 1988; Wenner 1992).

Adult wild red drum show a preference for oyster reefs over other habitat types, including seagrass, marsh, and unvegetated sand bottom (Stunz et al 2001). Larval red drum also consume larval molluscs. Holt and Holt (2000) found in their gut content study that in the Gulf of Mexico small red drum (<3 mm) primarily fed on copepod nauplii, bivalve larvae, and barnacle nauplii. Red drum have been collected in and around oyster reef habitats in Virginia and South Carolina (Table 2).

Scup (*Stenotomus chrysops*)

Scup is a small porgy of the family Sparidae. Both juvenile and adult scup utilize shellfish habitats for foraging and shelter purposes. Reefs are particularly important during the colder months when scup exhibit poor growth, because scup are inactive during this time and are in need of protective shelter. Juvenile scup have been observed using biogenic depressions, sand wave troughs, and possibly mollusc shells for shelter during the colder months (Steimle et al. 1999). Young-of-year scup have been collected over shell and mussel beds as well as other substrates. In addition to soft sandy bottoms, adult scup habitats include mussel beds, rocky ledges, wrecks, and artificial reefs (Steimle et al. 1999).

Shellfish habitat also provides scup with a food source. Juveniles feed on polychaetes, epibenthic amphipods, small crustaceans and molluscs, and fish eggs and larvae, which are abundant in and around shellfish reefs. Adult scup feed on bivalve molluscs (Steimle et al. 1999). Auster et al. (1995) state that juvenile scup utilize mussel beds in the deep areas of Long Island Sound. Scup are bottom feeders, generally remaining near the bottom, preying on cnidarians, squids, polychaetes, crustaceans, and fishes. Juvenile scup in Narragansett Bay feed on polychaetes, mysids and other crustaceans, molluscs, and fish eggs and larvae. Larger scup consumed molluscs (18%) (mainly squid, amphipods (6%), and decapods (2%)) (Bigelow and Schroeder 1953).

Adult scup form schools of similar-sized individuals over many bottom types. They are particularly abundant around piers, rocks, offshore ledges, jetties, and mussel reefs. They move inshore to southern coastal areas of Massachusetts in May and remain in the area until October, moving into deeper waters or migrating south to the waters ranging from Cape May, New Jersey to Cape Hatteras, North Carolina (Bigelow and Schroeder 1953). Along the Massachusetts coast, scup range in depth from 2-37 m (6-120 feet). Adult scup in this area feed on invertebrates including small crabs, annelid worms, clams, mussels, jellyfish, and sand dollars. Each year as many as 80% of all juvenile scup fall prey to larger predators such as cod, bluefish, and weakfish (MA DMF 2006).

Shad (American, *Alosa sapidissima* and hickory, *Alosa mediocris*) and river herring (alewife, *Alosa pseudoharengus* and blueback herring, *Alosa aestivalis*)

All of the managed *Alosa* species are primarily pelagic and anadromous, returning to riverine freshwater to spawn (Munroe 2002). Hard substrates of various kinds are important in the spawning of American shad and blueback herring. This suggests that, similar to Atlantic herring, shell accumulations might be important in some areas for egg deposition. Otherwise, little is known of their relationship to shellfish habitats. McCord (2005) provides a recent overview for the Alosines in southeastern U.S. waters with particular reference to status, threats, and challenges in South Carolina. One concern is competition and predation from non-native species such as flathead and blue catfish. Dredging is also of concern due to the effects of suspended sediments (McCord 2005).

Spanish mackerel (*Scomberomorus maculates*)

Spanish mackerel is a pelagic schooling species found along most of the U.S. Atlantic coast (Collette et al. 1978; Godcharles and Murphy 1986). The average weight of an individual of this small scombrid species is less than 3 lbs (maximum 9-10 lbs.); they can attain a maximum length of approximately 36 in. Spanish mackerel generally live from 5 to 8 years. During summer months, they are commonly found as far north as Chesapeake Bay; however, in fall and winter, they are most common in the waters off central and southern Florida. Spanish mackerel are typically found around ocean beaches and the lower reaches of estuaries (Godcharles and Murphy 1986). Juveniles are often collected from moderate salinity (13–20 ppt) areas within estuaries, as well as from higher salinity beaches, suggesting that they may utilize one or more estuarine habitats as nursery grounds (Springer and Woodburn 1960).

The diet of Spanish mackerel consists mainly of small fishes, along with penaied shrimp and cephalopods. As with several other ASMFC managed species, little specifics are known with regard to specific juvenile nursery habitats. However, Spanish mackerel have been collected on oyster reef habitats in Virginia, North Carolina, South Carolina, and Louisiana (Table 2).

Spiny dogfish (*Squalus acanthias*)

There is little information on relationships between spiny dogfish and shellfish habitat. However, molluscs typically make up a significant portion of their diet (Bowman et al. 2000). Spiny dogfish are opportunistic feeders, eating whatever prey is abundant. In general, their diet is comprised of small fishes, such as capelin, cod, haddock, hake, herring, menhaden, and ratfish. They also consume invertebrates, such as krill, crabs, polychaete worms, jellyfish, ctenophores, amphipods, squid, and octopus. Spiny dogfish are found in cold and temperate oceans at temperatures between 6 and 15°C, but can be found in waters with temperatures as low as 3°C. Spiny dogfish are tolerant of a wide range of salinities and can be found throughout estuaries to depths of 730 m (2,400 ft) in the ocean (Compagno 1984). Additionally, Schwartz and Porter (1977) collected spiny dogfish over a calico scallop aggregation in North Carolina.

Spot (*Leiostomus xanthurus*)

Several studies have shown that juvenile and adult spot utilize oyster reefs (Arve 1960; Breitburg 1999; Harding and Mann 2000; Coen et al 1999a). Juvenile spot collected around the reef indicate that the reefs are potentially important nursery grounds (Coen et al 1999b). Additionally, Breitburg (1999) stated that spot use oyster reefs for feeding on benthic invertebrates and fish that exist around the shell substrate. Arve (1960) found that an increase in planted oyster shells was positively correlated with the number of spot caught on the reef. Based on examination of 903 stomachs of fish from the Gulf of Mexico, Kobylinski and Sheridan (1979) found that bivalves made up 10.4% of their diet. In a gut content study in the Apalachicola Bay, Florida, Sheridan (1979) found that bivalves were the dominant prey items of spot ranging in size from 90 to 109 mm. Spot have been collected in and around oyster reef habitats in Maryland, Virginia, North Carolina, South Carolina, and Louisiana (Table 2).

Spotted seatrout (*Cynocion nebulosus*)

Spotted seatrout have been collected off oyster reefs and calico scallop aggregations where their larval forms feed on bivalve larvae. Schwartz and Porter (1977) caught spotted seatrout over calico scallop aggregations in the ocean off North Carolina. Holt and Holt (2000) found that larval spotted seatrout in the Gulf of Mexico consumed bivalve larvae in a gut content study. The study demonstrated that the most important prey for small (<3.0 mm) spotted seatrout were bivalve larvae, copepod nauplii, gastropod veligers, and dinoflaellates. For medium sized (3.0 - 4.5 mm) spotted seatrout larvae, the most important prey items were bivalve larvae, dinoflagellates, soft-bodied surface organisms, calanoid copepods, and soft-bodied bottom organisms and copepod nauplii. Large larval spotted seatrout (>4.5 mm) also fed on bivalve larvae on the surface (Holt and Holt 2000). *C. nebulosus* has been collected in and around oyster reef habitats in Virginia, North Carolina, and South Carolina (Table 2).

Striped bass (*Morone saxatilis*)

The striped bass is the largest member of the temperate bass family Moronidae. Striped bass are a coastal species that moves far upstream during spawning migrations in coastal rivers. The native range is the Atlantic coast from New Brunswick, Canada, south to north Florida, and from west Florida into Louisiana. Often juvenile striped bass, and sometimes adults, can be observed around oyster reef structures. In one study, an average of 15.4 individuals/m^2 reef surface were observed (Breitburg 1999). Shrimp and anchovies typically dominate their diet during the summer and fall, while the diet is composed of more fishes throughout the winter. Striped bass use reefs as a foraging ground; they feed on the larvae, juvenile, and adult naked gobies, and other resident fish species (Table 2) (Coen et al. 1999b). Due to high abundances, naked goby larvae are often considered to be the most important prey for juvenile striped bass (Breitburg 1999). A study by Schwartz and Porter (1977) collected striped bass over calico scallop beds in the ocean off North Carolina. Striped bass have been collected around oyster reefs in Maryland, Virginia, and North Carolina (Table 2).

Summer flounder (*Paralichthys dentatus*)

Summer flounder use shellfish habitats for protection and foraging grounds (NC DMF 2001). Surveys by Hoffman (1991) found that summer flounder were abundant in a variety of substrates, including mud, sand, shell hash, and oyster bars. Additionally, in studies conducted in New Jersey, Roundtree and Able (1992, 1997) reported summer flounder in high abundances over marsh creeks with mud bottoms and shell hash. Powell and Schwartz (1977) found the highest abundances of summer flounder over sand and shell. Summer flounder have been collected in and around oyster reefs in Maryland, Virginia, North Carolina, and South Carolina (Table 2).

Tautog (*Tautoga onitis*)

Tautog is fished both commercially and recreationally in the northeast and mid-Atlantic (Hostetter and Munroe 1993), with a range from Canada to South Carolina. Shellfish habitat is important to both juvenile and adult tautog. Oyster reefs, along with SAV and macroalgae, provide important nursery grounds for the juvenile fish. Oyster reefs also provide vertical relief and significant refuge for juveniles and adults. Young-of-year and juvenile fish utilize empty oyster shells, clam shells, and sponge as habitat. Adults are found on a variety of substrates including oyster and mussel beds, vegetation, rocks, artificial reefs, and shipwrecks (Dorf and Powell 1997; Olla et al. 1979; Sogard et al. 1992).

Molluscs also provide tautog with a source of food. One of the primary food sources of the tautog is the blue mussel (*Mytilus edulis*) (Grover 1982; Steimle and Shaheen 1999). A study by Steimle and Ogren (1982) found that blue mussels comprised more than 25% of the total stomach and intestine volume in tautog sampled on an artificial reef. Curran and Able (1998) tethered tautog and winter flounder in various estuarine habitats in New Jersey to assess relative predation rates in vegetated habitats, but little information has been gathered experimentally in shellfish habitats. Tautog have only been collected in and around oyster reefs in Virginia (Table 2), perhaps due to sampling bias in the mid-Atlantic region.

Weakfish (*Cynoscion regalis*)

Weakfish utilize shellfish reefs and aggregations and feed on molluscs. Several studies report weakfish as common around oyster reef habitat (Harding and Mann 1999, 2000; Lenihan et al. 2001; Coen et al. 1999b; SAFMC 1998b). Harding and Mann (1999a) indicate oyster reefs are important to weakfish as both feeding and nursery grounds. Additionally, they found that weakfish feed on blennies and gobies, which are primarily found on oyster reefs. Schwartz and Porter (1977) collected weakfish over calico scallop aggregations in North Carolina. Weakfish have been collected in and around oyster reefs in Virginia, North Carolina, and South Carolina (Table 2).

Winter flounder (*Pleuronectes americanus*)

Winter flounder use a diversity of shellfish habitats. They have been collected on reefs from Maryland and Virginia (Table 2). Howell and Molnar (1999) reported that mean catch of young-of- year flounder was highest in muddy sediments covered with shell. They also collected winter flounder on coot clam, mussel, gem shell, oyster, hard clam, and ark shell beds. Young-of-year winter flounder and adult winter flounder prey mostly on amphipods and polychaetes, which are found in high abundances on oyster and mussel reefs. Also, flounders are listed as probable predators of damaged scallops (Elner and Jamieson 1979). Shellfish habitats also provide the young-of-year winter flounder with protection from predators (Howell et al. 1999).

V. MANAGEMENT AND RESEARCH ISSUES

Managing Shellfish Habitats for Rebuilding and Sustaining Fisheries

The 1996 reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act (often referred to as the Sustainable Fisheries Act) defines essential fish habitat (EFH) as: *"those waters and substrates necessary to fish for spawning, feeding, breeding and growth to maturity."* The above review shows that shellfish habitats are important to many of the ASMFC-managed species, and probably should be considered EFH for some. Although the knowledge base is limited, there is sufficient information to understand some of the relationships between shellfish habitats and managed species that are important for policy development.

The most important ecological characteristics of shellfish habitats are hard substrate, vertical structure, and food supply. These characteristics are the basis for the major ecological services provided by shellfish habitats (refuge, benthic-pelagic coupling, and erosion control) as well as the basis for the importance shellfish reefs, aggregations, and shell accumulations to many managed species. The overall result is a significant enhancement of habitat value for many species in Atlantic shelf, coastal, and estuarine waters. Therefore, conservation and restoration of these characteristics and services should greatly benefit many ASMFC-managed species.

Remote Sensing and Other Distributional Databases

Shellfish habitats are typically managed by individual states, which have their own distributional databases and management policies. The most information is available for species such as oysters that have been managed historically as a food resource, but now also as an ecological resource. However, some information exists for all types of shellfish habitats. These databases will form the basis of management at higher levels. Although many states have these types of databases (see recent work in Florida by Gambordella et al. 2007), the following descriptions from South Carolina, North Carolina, and New Hampshire are presented as examples. A more comprehensive review is underway (R. Grizzle and L. Coen, personal statement).

South Carolina database

South Carolina has extensive information on distributions of oysters, ranging from surveys completed in 1890-91 (Battle 1891) to maps based on recent aerial imagery (NOAA CSC 2003; Schulte et al. 2005). South Carolina Department of Natural Resources (SCDNR) completed a statewide intertidal oyster resource assessment from 1980 to 1987, with periodic reassessments through the present day (Jefferson et al. 1991). This intertidal oyster survey measures each oyster population using laser or split image rangefinders to determine the reef's dimensions. Global Positioning System (GPS) coordinates are taken in the center of each reef, the area is digitized, and later coordinates are entered into the SCDNR's shellfish management Geographic Information System (GIS). Ancillary data, including temperature, salinity, shell matrix depth, reef elevation, adjacent water depth, dead vs. live oysters, etc. are collected and utilized for management purposes. Oyster populations are categorized by characteristic spatial dispersions (densities) that allow an estimate of each reefs' standing stock (Jefferson et al. 1991).

For a new remote sensing approach, SCDNR is collaborating with NOAA's Coastal Services Center and several contractors to apply earlier developed methods using airborne multispectral digital imagery acquired by GeoVantage Inc.'s GeoScanner system (Figure 6). Photo Science (a SCDNR contractor) is deriving results including location, extent, and condition of intertidal oyster populations along coastal areas of South Carolina. Field assessments are being conducted in order to ground-truth these results and assist in development of extraction techniques. GPS data are collected as linear representations (transects) of intertidal oyster populations. Oyster density, reef size (or footprint), and location data are collected in the field, along with video. The information is available via the SCDNR's GIS Data Clearinghouse (http://www.dnr.sc.gov/pls/gisdata/download_data.login).

North Carolina database

As summarized in Street et al. (2005), the North Carolina Division of Marine Fisheries (NC DMF) Shellfish Habitat and Abundance Mapping Program began in 1988, when detailed bottom type maps were created using standard surveys from the Cape Fear area through Core Sound, along the perimeter of Pamlico Sound, and in Croatan/Roanoke sounds. All bottom habitats, including shell bottom, are currently being delineated, with samples collected of molluscan densities that differentiate 24 different bottom types based on combinations of depth, bottom firmness, vegetation density, and density of surface shells. An area is determined to be shell habitat (or shell bottom) if more than 30% of the bottom sampled is composed of living shellfish and dead shell. Mapping is still in progress as of 2006. Maps and data files are available upon request to NC DMF.

New Hampshire database

Managed shellfish species in New Hampshire include oysters, mussels, and softshell (*Mya arenaria*) clams. Distributional data are available for all three species, although historical information (pre-1980s) is meager, with oysters being the primary focus. Ongoing mapping programs (Grizzle et al. 2005, 2006) are in part research-oriented and include multibeam sonar, underwater videography, and extractive sampling methods (Figure 2). All oyster reefs occur subtidally, so aerial imagery cannot be used for mapping. Similar efforts have proven useful with other shellfish species (Goshimam and Fujiwara 1994; Powell et al. 1995; Smith et al. 2001; Morrison and Carbines 2006).

The New Hampshire Fish and Game Department (NH FGD) has primary management responsibility for shellfish, but other state agencies are also involved. Mapping efforts for both clams and oysters have recently been funded through collaborative projects involving NH FGD, the NH Estuaries Project, the Nature Conservancy, and the University of New Hampshire (UNH). All maps that result from these projects are GIS-based, and some are available via the Internet (Grizzle and Brodeur 2004). An ongoing Sea Grant-funded project is aimed at development of a general protocol involving sonar and videography that can be tested in other areas for mapping subtidal oyster reefs.

Recently, a research project supported by the NOAA/UNH Cooperative Institute for Coastal and Estuarine Environmental Technology (CICEET) completed a study evaluating hyperspectral imagery (including LiDAR) as approaches for mapping, monitoring, and managing intertidal shellfish populations (Schill et al. 2006; Vincent 2006). Although more expensive than multispectral approaches, hyperspectral imagery shows promise as the technology becomes more widely accessible.

Relationship Between Shellfish Habitat and User Species

Many of the organisms found on the shellfish reefs are not found on adjacent sand or mud habitats (Coen et al. 1999b). Oyster reefs are especially important from southern North Carolina to northeast Florida because these areas have little or no submerged aquatic vegetation (Coen et al. 1999a). Therefore, oyster reefs provide the only extensive structurally complex estuarine habitat available in these areas (Eggleston et al. 1998; Coen et al. 1999b).

Many studies have also demonstrated that oyster reefs, as three-dimensional structures, attract more resident and transient species than mud or sandy substrates. Harding and Mann (2001) found that in the Piankatank River, Virginia, more bluefish were found on oyster reef sites than on non-reef sites. In their study, twice as many fish were found on oyster reefs than on surrounding sand bars (Harding and Mann 2001a). Lenihan et al. (2001) showed that in the Neuse River estuary, North Carolina, fish abundance and species richness were two to three times higher on oyster reefs than on sand substrates. Additionally, pinfish, blue crabs, and grass shrimp were found in greater abundance over the oyster reefs compared to adjacent sandflats (Posey et al. 1999).

We note here that less work has been done on quantifying mobile species over unstructured mudflats and sandy bottoms (Beck et al. 2001, 2003; Lenihan and Micheli 2001). Sandy beaches, mudflats, and sandflats are especially important in providing feeding areas for a variety of waterfowl, particularly migratory waders (Thayer et al. 2005). We do not mean to suggest that these habitats are of lower value (e.g., see Coen et al. 2006a who quantitatively sampled adjacent oyster, fringing marsh, and mudflats using lift nets), rather, that our focus in this review is on shellfish dominated habitats. For additional information, see reviews by Boesch et al. (1994), Peterson and Peterson (1979), Reise (1985), Alongi (1997), Kaiser et al. (2000), Olafsson and collaborators (1994, 2003), Micheli (1996), and additional references in Lenihan and Micheli (2001) and Thayer et al. (2005). More work on unstructured habitats has probably been done outside of the United States in Europe, Australia, and New Zealand, but efforts within the U.S. have been increasingly supporting the notion that mudflats and sandy intertidal and subtidal habitats, adjacent to more structured and better known habitats, have a much greater value then previously understood (R. Grizzle, personal statement).

At least seven species of fish have been identified as resident species on oyster reefs, meaning that they depend on the reefs for breeding and feeding habitat, as well as for shelter from predators (Table 2) (Coen et al. 1999b). The seven resident species are the naked goby, striped blenny, feather blenny, freckled blenny, skilletfish, oyster toadfish, and gulf toadfish. Toadfish attach their eggs to the underside of consolidated oyster shells, and skilletfish, blennies, and gobies lay their eggs in recently dead oyster shells (Breitburg 1999; Coen et al. 1999a).

While not exclusively resident to oyster reefs, many other organisms use the oyster reef as habitat (Coen et al. 1999a, 1999b; Glancy et al. 2003; Luckenbach et al. 2005; Tolley and Volety 2005; Kimbro and Grosholz 2006; Rodney and Paynter 2006; Walters and Coen 2006). Wells (1961) collected three hundred and three species on oyster reefs. Dame (1979) found thirty-seven species on South Carolina reefs; Bahr and Lanier (1981) observed a total of fortytwo species of macrofauna, representing seven phyla, on the reefs in Georgia. On the Delaware Bay, Maurer and Watling (1973) identified one hundred and fifty-two species associated with oyster reefs.

In related efforts on the same reefs in South Carolina (Coen et al. 1999a, 1999b, 2006; Coen and Luckenbach 2000; Luckenbach et al. 2005; Walters and Coen 2006), researchers studied communities utilizing natural and man-made intertidal oyster reefs. Transient finfish and macroinvertebrates collected at two sites yielded over 59 species; similarly, resident macroinvertebrates totaled more than 75 species. Additionally, Rodney and Paynter (2006) recently observed increased abundance and biodiversity on restored oyster reefs compared with non-restored reefs (Table 2).

A group of important species that are largely understudied throughout their range, but includes important members of intertidal and subtidal oyster reef communities, are the grass (Caridean) shrimp species within the genus *Palaemonetes.* Grass shrimp are found in large numbers in estuarine waters along the Atlantic and Gulf coasts, where they occur from Massachusetts to Texas. They are a very common estuarine species in southeastern marshes and tidal creeks where they are usually associated with beds of submerged or emergent vegetation, oyster reef habitats, or structures such as oyster shell, fouling communities, woody debris (Ruiz et al. 1993), and docks or pilings (Coen et al. 1981). Caridean shrimp are rarely larger than 5 cm; their small size differentiates them from commercial shrimp, such as the penaieds and pendalids.

Grass shrimp are an important species from an ecological perspective because they are instrumental in transporting energy and nutrients between trophic levels in the coastal food web. Grass shrimp are consumed in large quantities by commercially important fishes and forage species, including spotted seatrout, red drum, and mummichogs (*Fundulus heteroclitus*) (Heck and Thoman 1981; Anderson 1985; Wenner et al. 1990; Posey and Hines 1991; Wenner and Archambault 1996).

Although there are no estimates of population sizes of grass shrimp, they are amongst the most widely distributed, abundant, and conspicuous of the shallow water benthic macroinvertebrates in our estuaries, often reaching hundreds to thousands per square meter (Leight et al. 2005; Coen and Luckenbach 2000; Coen et al. 2006a). Grass shrimp can inhabit very shallow areas near the margins of intertidal habitats (e.g., marsh, mudflats, oyster reefs), but have been reported at depths as great as 15 meters. In winter during temperature lows, and in summer when water temperatures approach seasonal highs, daggerblade grass shrimp may move from shallow to relatively deeper water. The extent of the movement of grass shrimp among various depths often coincides with the distribution of oyster shell substrates, which, in some waters, are preferred by both *P. vulgaris* and *P. pugio*. They are abundant in these structured estuarine and marine habitats as shellfish habitats provide abundant food and protection from predators (Thorp 1976; Coen et al. 1981; Heck and Thoman 1981; Heck and Crowder 1991). Consequently, the association of shellfish habitats with primary producers and consumers may prove quite significant, given the importance of low trophic level species as food for managed species.

Oyster reefs are also a foraging ground for many juvenile and adult turtle species. Schmid (1998) found that both the Kemp's ridley and loggerhead sea turtles feed on organisms that inhabit the reef. Kemp's ridley turtles feed on the stone crabs (*Menippe* spp.) and blue crabs

(*Callinectes sapidus*) found near the reef's surface. Loggerheads also feed on molluscs. Schmid (1998) also found that Kemp's ridleys will return to the same oyster reef for up to four years.

Another important species that utilizes intertidal and subtidal oyster reefs as foraging grounds is the blue crab, *Callinectes sapidus* (Coen et al. 1999b). Blue crabs forage heavily on oyster reefs (Mann and Harding 1997; Krantz and Chamberlin 1978), including consuming oyster spat as juveniles. A study by Menzel and Hopkins (1955) showed that juvenile blue crabs consumed as many as 19 juvenile oysters (or spat) per day.

Shell accumulations also provide important nursery habitat for many species. For example, it has been noted in South Carolina that the preferred habitat of juveniles of several drum species is high marsh with shell hash and mud bottoms (Daniel 1988). As previously mentioned, 'washed oyster shell', especially along the edges of the Intracoastal Waterway (ICW), may also be important (Anderson et al. 1979). Additionally, planted shell may enhance the value of many areas as nurseries, paralleling artificial reef efforts (Coen and Luckenbach 2000; Lehnert and Allen 2002; Sanders et al. 2004; Coen et al. 2005).

Numerous mammals and birds directly and indirectly utilize intertidal oyster reef habitats and washed oyster shell accumulations, particularly along the IWW (Sanders et al. 2004). Some recent observations in SC suggest that a single oystercatcher may be able to consume over 100 adult oysters per day on intertidal reefs (F. Sanders, South Carolina Department of Natural Resources, personal communication). These include *Procyon lotor* (raccoon), and birds such as *Haematopus palliates* (American oyster catcher) (Figure 1a- Plate D), *Egretta tricolor* (Tricolored Heron), *Nyctanassa violacea* (Yellow-crowned Night Heron), *Nycticorax nycticorax* (Black Heron), *Casmerodius albus* (Great Egret), *Egretta thula* (Snowy Egret), *Limosa fedoa* (Marbled Godwit), *Catoptrophorus semipalmatus* (Willet), *Pluvialis squatarola* (Black-bellied Plover), *Calidris pusilla* (Semipalmated Sandpiper), *Calidris mauri* (Western Sandpiper), *Arenaria interpres* (Ruddy Turnstone), *Tringa melanoleuca* (Greater Yellowleg), and *Tringa flavipes* (Lesser Yellowleg).

Shellfish Restoration Programs

Shellfish restoration projects are underway in many areas along the U.S. Atlantic coast. They range from multi-million dollar collaborative efforts in the Chesapeake Bay region involving state agencies, federal agencies, and NGOs, to smaller community-based projects in many areas. In several cases, emphasis has shifted from resource restoration to a broader ecological function perspective (Coen et al. 1999a; Hargis and Haven 1999; Luckenbach et al. 1999; Coen and Luckenbach 2000; French McCay et al. 2003; Peterson and Lipcius 2003; Nestlerode 2004; Luckenbach et al. 2005). Recently, broader ecological questions (e.g., scale, habitat complexity, facilitation, ecosystem valuation, and population structure, including genetics) have been addressed (Osman et al. 1989; Stephens and Bertness 1990; Luckenbach and Paige 2003; Peterson and Lipcius 2003; Peterson et al. 2003; Milbury et al. 2004).

In New York, The Nature Conservancy (TNC) and the Bluepoints Bottomlands Council are working to restock 13,000 acres of TNC's underwater holdings in Great South Bay with adult hard clams and establishing spawner sanctuaries. During the 1970s, hard clams filtered 40% of the entire volume of Great South Bay each day. Today, there are only enough hard clams to filter 1% of this vast body of water each day (K. Chytalo, New York Department of Environmental Conservation, personal communication). TNC is also establishing hard clam and bay scallop spawner sanctuaries in Peconic Bay in conjunction with New York state and Cornell Cooperative Extension. These efforts build off of New York Sea Grant's Hard Clam Initiative, which investigated the population dynamics of hard clams in Long Island's south shore estuary (K. Chytalo, New York Department of Environmental Conservation, personal communication).

As noted above, projects aimed at ecological restoration of shellfish habitat are relatively recent. North Carolina's first ecological oyster reef restoration project did not occur until the early 1990s, when 13 acres of oyster-producing habitat were created as mitigation for a federal dredging project which caused the loss of 16 acres of estuarine bottoms and 1.5 acres of wetlands in Roanoke Sound (Marshall et al. 1999). More recently, the North Carolina Department of Marine Fisheries has performed mitigation projects for the North Carolina Department of Transportation, and additional projects creating more than 70 acres of shell bottom are planned with the U.S. Army Corps of Engineers (Marshall et al. 1999).

A large amount of research effort is currently being given to the question of how to best construct and monitor oyster habitats (Coen and Luckenbach 2000; Thayer et al. 2003, 2005; Brumbaugh et al. 2006; Coen et al. 2007; S. Morlock, NOAA Restoration Center, personal communication; M. Posey, University of North Carolina at Wilmington, personal communication). Luckenbach et al. (2005) and Coen et al. (2006a, 2007) suggest that evaluations of restoration efforts need to move away from fisheries-dependent metrics and towards the use of ecological measures of success.

Smaller-scale reefs have also been constructed in many states using volunteer labor through community restoration efforts that are often supported by NOAA's Community Restoration Program (CRP), FishAmerica, and other programs (Brumbaugh et al. 2000a, 2000b, 2006; Hadley and Coen 2002; Leslie et al. 2004; Thayer et al. 2003, 2005). Although the acreage is often small, relative to large-scale efforts for resource or habitat restoration, the return can be significant in terms of generating matching funds and volunteer hours, educational efforts, and public support for funding the projects (e.g., oyster gardening, shell bag planting) (Brumbaugh et al. 2000a, 2000b, 2006; Hadley and Coen 2002; Coen et al. 2006b). The South Carolina Oyster Restoration Enhancement Program (SCORE), The Nature Conservancy (TNC, Restore America's Estuaries (RAE) the Chesapeake Bay Foundation, and other NGOs are all making significant strides in community reef restoration.

Restoration of shellfish habitats must be accompanied by sufficient protective measures to prevent further loss of these habitats (Kaufman and Dayton 1997; Luckenbach et al. 1999, 2005; Caddy and Defeo 2003; Jordan and Coakley 2004; Kirby 2004). Overfishing and habitat destruction have been cited as primary causes of the decline of Chesapeake Bay oysters to about 1% of historical levels (Newell 1988, 2004; Rothschild et al. 1994; Boesch et al. 2001a, 2001b; Jackson et al. 2001; Peterson et al. 2001b; Kirby 2004; Smith et al. 2005). Without reductions in the nutrient loadings that are driving phytoplankton blooms and related eutrophication in estuaries where shellfish are abundant, restoration of benthic suspension-feeders will only solve some of the current problems (Gerritsen et al. 1994; Pomeroy et al. 2006). As Breitburg and Fulford (2006) have verified, non-bivalve invertebrate suspension feeders will also be enhanced by the presence of healthy and extensive subtidal shellfish habitats (Gerritsen et al. 1994; Boesch et al. 2001a, 2001b; Jackson et al. 2001; Peterson et al. 2001b; Smith et al. 2005). Benthic communities in poor condition often occur in areas of environmental degradation proximate to highly populated coastal areas (EPA 2004). Therefore, additional regulatory controls may be needed to protect these habitats.

VI. FUTURE RESEARCH AND KNOWLEDGE GAPS

Here we summarize feedback from researchers and managers throughout the Atlantic and Gulf coasts (see Acknowledgements Section for contributors) regarding molluscan species and related habitats. The major topics mentioned included the impacts of global climate change on shellfish and their habitat, as well as hurricanes, cascading ecosystems, introduced or invasive species, anthropogenic disturbances, water diversions or re-diversions, overharvesting, disease, and interactions among these areas. The following knowledge gaps and research recommendations are included to focus shellfish habitat research efforts. Shumway and Kraueter (2004) also look at potential and interesting avenues of research, including management issues for molluscan shellfish. The following are not ranked in any particular order.

Baseline Information

- Evaluate the health, population status, and distribution of hard clams in Atlantic coast states
- Evaluate the health, population status, distribution, and species composition of pen shell habitats in Atlantic coast states
- Examine the recent dramatic declines of surfclam stocks in the mid-Atlantic region
- Support research on less apparent species, such as nucleus scallops (*Argopecten nucleus*) and calico scallops (*Argopecten gibbus*), which may provide the only substrate and structure in an otherwise depauperate shelf habitat
- Examine the relatively unknown functions of Atlantic surfclam (*Spisula solidissima*) shell beds
- Determine the minimum abundance or density needed for a shellfish population to be self-sustaining, support a fishery, and provide measurable ecological value
- For oysters and scallops (especially *Argopecten irradians*), compile information on larvae size, spatial distributions, and recruitment intensities
- Compare the different ecological services provided by fished, unfished, and aquaculture populations of shellfish species
- Determine the relative value of the three types of shellfish habitat (reefs, aggregations, and accumulations)
- Determine what characteristics of shellfish habitats should be considered in fishery management
- Examine age structure, growth rates, and natural mortality rates in important bivalve populations across species ranges, including spatial and temporal elements of recruitment
- Examine long-term changes in bathymetric and latitudinal distributions of shellfish populations relative to climate change
- Obtain genetic information for species in isolated or fragmented habitats to examine metapopulation dynamics
- Survey benthic shellfish habitats to quantify and map changing seascapes

- Determine the minimum freshwater flow input needed to estuaries to support historic populations of oysters

Health Issues

- Determine how changes in water quality influence the spread of shellfish diseases
- Examine causes of the varied effects of toxins from harmful algal blooms on different shellfish species
- Determine why some shellfish species purge intact and viable harmful algae while others do not
- Examine the importance of *Ostreola (=Ostrea) equestris* as habitat and as a disease carrier/host for harmful protistan parasite species (e.g., *Bonamia* spp.), particularly in subtidal areas where *Crassostrea virginica* is excluded
- Evaluate if *Ostreola (=Ostrea) equestris*' natural ecosystem function is threatened by parasites such as *Perkinsus* and *Bonamia*
- Further examine the potential of molluscan species to be used as "sentinel species" for determination of potential environmental impacts and community health

Community Relationships

- Evaluate the capacity of standing biomass of molluscan species in a given area to affect water quality and overall community structure (e.g, pelagic–benthic coupling)
- Determine the relationships between the amount of living and dead shell bottom and the condition of that shell bottom, to changes in community structure
- Quantify the contribution (and spatial extent) of dense bivalve populations' filtration activities to lowering turbidity, including how that reduction directly and indirectly influences SAV cover and health
- Evaluate the importance of pen shells, especially dead *in situ* pen shells, as refuge for mobile invertebrates and small fishes, sediment stabilizers, and members of the trophic cascade
- Evaluate if increased harvesting of ribbed mussels from marsh habitats impacts the functioning of those habitats
- Evaluate the impact of green mussels on fouling communities and oyster reefs
- From a fishery standpoint, examine periodicity in year-class structure of shellfish populations, particularly in relation to natural and/or fishing mortality
- Determine if the extirpation of bay scallop (*Argopecten irradians*), at some locations has been compensated for by an increase in slipper shells (*Crepidula* spp.); compare findings to occurrences in France, where introduction of slipper shells with oysters has likely caused significant problems for native bivalve species

- Evaluate how the introduction and spread of green and asian crabs impacts native shellfish species
- Determine the relative contribution of non-shellfish organisms to water quality and planktonic communities
- Evaluate the use of shell bottom by ASMFC-managed species via gut content analysis

Restoration

- Examine how climate change and variability, water quality, interactions with predators, and/or changes in population dynamics vary in restored versus unrestored sites
- Compile the results of *Crassostrea virginica* restoration efforts throughout the species' range, with particular emphasis on the outcomes and observations of projects that have been conducted for more than three years
- Develop protocols to prioritize research on the restoration of shellfish habitat in areas stressed by disease, over-fishing, and habitat degradation
- Evaluate how the harvesting of shell (e.g., dredging) impacts shellfish habitat restoration efforts
- Evaluate the effects of planting shell on existing habitats (e.g., habitat exchange)

Environmental Change

- Evaluate how global climate change affects molluscan species in general, and species like the surf clam in particular
- Determine if global climate change and novel exotic species affect molluscan habitat-engineers and related species
- Evaluate how bivalve diet selection for certain microalgal species may preferentially stimulate one microalgal group over another, thereby affecting harmful algal blooms (HABs) either by releasing nutrients or moving HABs

Habitat Indicators

- Develop indicators of shell habitat condition, and determine various shellfish (managed or non-fishery) species that are appropriate indicators of shell 'habitat' condition. Collect fishery-independent data for these potential indicator species to complement fishery-dependent data (landings data) for use in development of independent condition indices

Aquaculture

- Determine the carrying capacity of cultured species as it relates to natural ecosystem impacts and/or contribution
- Examine the impacts of movement and dilution of natural genetic stocks due to aquaculture introductions

VII. TABLES AND FIGURES

Tables

Figures

Table 1. Summary of shellfish habitat use for the 22 ASMFC-managed species. Habitat Type abbreviations: mussel reefs (MR), oyster reefs (OR), shell accumulations (SA), and scallop aggregations (Sc). Life stage abbreviations: young-of-year (YOY), juvenile (J), and adult (A).

Fish Species	Habitat Type	Use	Life Stage	Reference
American eel *Anguilla rostrata*	OR	Found on reef, consume shellfish	YOY, J, A	Wenner and Musick 1975; Stewart 1972
American lobster *Homarus americanus*	(All)	Foraging ground, shelter	J, A	Weiss 1970; Miller et al. 1971; Ennis 1973; Elner and Jamieson 1979; Newell 1989; Auster et al 1991, 1995
Atlantic croaker *Micropogonias undulatus*	OR, Sc	Foraging ground	Not stated	Schwartz and Porter 1977; NC DMF 2001; Lehnert and Allen 2002
Atlantic herring *Clupea harengus*	SA	Reproduction	A	Messieh 1988; Reid et al. 1999
Atlantic menhaden *Brevoortia tyrannus*	OR	Found on reef	Not stated	Arve 1960
Atlantic sturgeon *Acipenser oxyrinchus*	SA	Reproduction, foraging ground	A	Dean 1894; Gilbert 1989; Smith and Clugston 1997; NMFS 1998; Collins et al. 2000
Black sea bass *Centropristis striata*	(ALL)	Nursery, shelter, foraging ground	YOY, J, A	Arve 1960; Schwartz and Porter 1977; Able et al. 1995; Able and Fahay 1998; Steimle et al. 1999
Bluefish *Pomatomus saltatrix*	OR, SA, Sc	Foraging ground	J	Schwartz and Porter 1977
Horseshoe crab *Limulus polyphemus*	MR, SA	Foraging ground	A	Botton and Haskin 1984; Botton and Ropes 1989
Northern shrimp *Pandalus borealis*	No data	No data	No data	No data
Red drum *Sciaenops ocellatus*	OR, SA	Nursery, foraging ground	YOY, J	Daniel 1988; Wenner 1992; SAFMC 1998; ASMFC 2002; Holt and Holt 2000; Stunz et al 2001
Scup *Stenotomus chrysops*	MR, SA	Shelter, foraging ground	YOY, J, A	Auster et al. 1995 ; Steimle et al. 1999
Shad and River herring *Alosa* spp.	No data	No data	No data	No data
Spanish mackerel *Scomberomorus maculatus*	No data	No data	No data	See Table 2
Spiny dogfish *Squalus acanthias*	Sc	Not stated	Not stated	Schwartz and Porter 1977
Spot *Leiostomus xanthurus*	OR	Nursery, foraging ground	J	Arve 1960; Kobylinski and Sheridan 1979; Sheridan 1979; Breitburg 1999
Spotted seatrout *Cynoscion nebulosus*	OR, Sc	Foraging ground	YOY	Schwartz and Porter 1977; Wenner and Archambault 1996; Holt and Holt 2000
Striped bass *Morone saxatilis*	OR, Sc	Foraging ground	J, A	Schwartz and Porter 1977; Breitburg 1999
Summer flounder *Paralichthys dentatus*	OR, SA	Shelter, foraging ground	Not stated	Powell and Schwartz 1977; Hoffman 1991; Roundtree and Able 1992, 1997; NCDMF 2001
Tautog *Tautoga onitis*	MB, OR, SA	Shelter, foraging ground	J, A	Steimle and Ogren 1982; Steimle and Shaheen 1999
Weakfish *Cynoscion regalis*	OR, Sc	Nursery, foraging ground	J	Schwartz and Porter 1977; SAFMC 1998
Winter flounder *Pseudopleuronectes americanus*	(ALL)	Nursery, foraging ground	YOY, A	Elner and Jamieson 1979; Howell et al 1999

Table 2. Fishes and decapods found on intertidal or subtidal oyster reefs or in waters directly overlying these reefs at various southern coastal locations. Facultative residents are species in which some, but not all, individuals remain on the oyster reef for several months. Some species listed as transients may actually be facultative residents (exclusive of South Carolina and Florida intertidal species). However they are highly mobile within the reefs, and the duration of residency of individuals has not been studied. Differences in species richness and composition among sites will likely reflect differences in collection methods as well as true differences in the fish and crustacean assemblages.

Common name (*Scientific name*)	**MD[1]**	**MD[2]**	**VA[1]**	**VA[2]**	**VA[3]**	**NC**	**SC[1]**	**SC[2]**	**FL[1]**	**FL[2]**	**LA**	**TX**
<u>Oyster Reef Resident Fishes</u>												
feather blenny (*Hypsoblennius hentz*)	X	X		X	X	X		X	X		X	
freckled blenny (*Hypsoblennius ionthas*)												X
gulf toadfish (*Opsanus beta*)									X		X	X
naked goby (*Gobiosoma bosc*)	X	X	X	X	X	X	X	X	X	X	X	X
oyster toadfish (*Opsanus tau*)	X	X	X	X	X	X	X	X		X		
skilletfish (*Gobiesox strumosus*)	X	X	X	X	X	X			X	X	X	X
striped blenny (*Chasmodes bosquianus*)	X	X	X	X	X	X	X	X			X	X
<u>Facultative Resident Fishes</u>												
Atlantic spadefish (*Chaetodipterus faber*)	X		X		X	X		X			X	
black sea bass (*Centropristis striata*)*	X		X	X	X	X						
darter goby (*Ctenogobius boleosoma)*							X	X			X	
northern pipefish (*Syngnathus fuscus*)	X			X			X	X				
seaboard goby (*Gobiosoma ginsburgi*)				X								
<u>Transient Fishes</u>												
American eel (*Anguilla rostrata*)*	X	X	X		X	X		X				
Atlantic bumper (*Chloroscombrus chrysurus*)								X				
Atlantic croaker (*Micropogonias undulatus)* *		X	X	X	X	X	X	X			X	
Atlantic cutlassfish (*Trichiurus lepturus*)				X								
Atlantic herring (*Clupea harengus*) *				X								
Atlantic menhaden (*Brevoortia tyrannus)* *		X	X		X	X	X	X				

Transient Fishes Continued	**MD[1]**	**MD[2]**	**VA[1]**	**VA[2]**	**VA[3]**	**NC**	**SC[1]**	**SC[2]**	**FL[1]**	**FL[2]**	**LA**	**TX**
Atlantic needlefish (*Strongylura marina*)								X				
Atlantic silverside (*Menidia menidia*)	X						X	X				
Atlantic stingray (*Dasyatis sabina*)							X	X				
Atlantic thread herring (*Opisthonema oglinum*)					X			X				
bantail puffer (*Sphoeroides spengleri*)								X				
bay anchovy (*Anchoa mitchilli*)			X	X	X		X	X				X
bay whiff (*Citharicthys spilopterus*)							X	X				
bighead searobin (*Prionotus tribulus*)						X	X	X				X
black drum (*Pogonias cromis*)				X		X		X			X	
blackcheek tonguefish (*Symphurus plagiusa*)				X			X	X		X		
blueback herring (*Alosa aestivalis*)			X									
bluefish (*Pomatomus saltatrix*) *****		X	X	X	X	X		X			X	X
bluntnosed stingray (*Dasyatis say*)					X							
brown bullhead (*Ameiurus nebulosus*)		X										
butterfish (*Peprilus triacanthus*)			X			X		X				
carp (*Cyprinus carpio*)			X									
chain pipefish (*Syngnathus louisianae*)							X	X				
channel catfish (*Ictalurus punctatus*)		X										
clown goby (*Microgobius gulosus*)										X		
cobia (*Rachycentron canadum*)			X									
code goby (*Gobiosoma robustum*)									X	X		
cownose ray (*Rhinoptera bonasus*)	X		X		X	X					X	
crested blenny (*Hypleurochilus geminatus*)								X			X	
crested goby (*Lophogobius cyprinoides*)									X			
crevalle jack (*Caranx hippos*)								X				
dusky pipefish (*Syngnathus floridae*)					X			X				
dwarf pipefish (*Cosmocampus hildebrandi*)										X		
Florida blenny (*Chasmodes saburrae*)									X	X		
Florida pompano (*Trachinotus carolinus*)								X				

Transient Fishes Continued	**MD[1]**	**MD[2]**	**VA[1]**	**VA[2]**	**VA[3]**	**NC**	**SC[1]**	**SC[2]**	**FL[1]**	**FL[2]**	**LA**	**TX**
fourspine stickleback (*Apeltes quadracus*)				X								
freshwater goby (*Ctenogobius shufeldti*)								X				
frillfin goby (*Bathygobius soporator*)									X	X		
fringed flounder (*Etropus crossotus*)								X				
gafftopsail catfish (*Bagre marinus*)											X	
gag (*Mycteroptera microlepis*)				X		X		X				
gizzard shad (*Dorosoma cepedianum*)					X							
glass eel (*Conger oceanicus*)				X								
goldspotted killifish (*Floridichthys carpio*)										X		
gray/mangrove snapper (*Lutjanus griseus)*						X	X	X	X			
great barracuda (*Sphyraena barracuda*)								X				
green sunfish (*Lepomis cyanellus*)												X
gulf killifish (*Fundulus grandis*)				X			X			X		
gulf menhaden (*Brevoortia patronus*)											X	X
gulf pipefish (*Syngnathus scovelli*)										X		
hardhead catfish (*Ariopsis felis*)											X	
harvestfish *(Peprilus paru)*			X			X		X				
highfin blenny (*Lupinoblennius nicholsi*)									X			
highfin goby (*Gobionellus oceanicus*)								X				
hogchoker (*Trinectes maculatus*)		X	X		X							
horse-eye jack (*Caranx latus*)								X				
inland silverside *(Menidia beryllina*)							X					X
inshore lizardfish (*Synodus foetens*)	X				X	X		X		X		
ladyfish (*Elops saurus*)								X				
lane snapper (*Lutjanus synagris*)								X	X			
leopard searobin (*Prionotus scitulus*)										X		
lined seahorse (*Hippocampus erectus)*			X	X	X							
lined sole (*Achirus lineatus*)										X		
lookdown (*Selene vomer*)				X		X		X				

Transient Fishes Continued	**MD[1]**	**MD[2]**	**VA[1]**	**VA[2]**	**VA[3]**	**NC**	**SC[1]**	**SC[2]**	**FL[1]**	**FL[2]**	**LA**	**TX**
lyre goby (*Evorthodus lyricus*)							X					
mahogany snapper (*Lutjanus mahogoni*)							X					
mojarra (*Eucinostomus* sp.)									X	X		
mummichog (*Fundulus heteroclitus*)								X				
northern puffer (*Sphoeroides maculatus*)			X		X			X				
northern searobin (*Prionotus carolinus*)			X	X								
northern stargazer (*Astroscopus guttatus*)								X				
ocellated flounder (*Ancylopsetta quadrocellata*)								X				
orange filefish (*Aluterus schoepfii*)							X					
permit (*Trachinotus falcatus*)								X				
pigfish *(Orthopristis chrysoptera)*			X	X		X	X	X		X		
pinfish (*Lagodon rhomboides*)	X		X			X	X	X	X	X	X	X
planehead filefish (*Stephanolepis hispidus*)							X	X				
pygmy filefish (*Stephanolepis setifer*)						X						
rainwater killifish (*Lucania parva*)				X								
red drum (*Sciaenops ocellatus) **					X		X	X				
rough silverside (*Membras martinica*)				X	X							
sailfin molly (*Poecilia latipinna*)								X				
sand seatrout (*Cynoscion arenarius*)											X	
sheepshead (*Archosargus probatocephalus)*				X	X	X	X	X	X	X	X	X
sheepshead minow (*Cyprinodon variegatus*)							X	X	X	X		
silver perch (*Bairdiella chrysoura*)			X	X		X	X	X	X	X	X	
southern flounder (*Paralichthys lethostigma)*						X	X	X				
southern kingfish (*Menticirrhus americanus*)											X	
southern stingray (*Dasyatis americana*)								X				
Spanish mackeral *(Scomberomorus maculatus)**			X			X		X			X	
speckled worm eel (*Myrophis punctatus*)							X	X		X		X
spot (*Leiostomus xanthurus*) **	X	X	X	X	X	X	X	X			X	
spotfin butterflyfish (*Chaetodon ocellatus*)				X								

Transient Fishes Continued	**MD[1]**	**MD[2]**	**VA[1]**	**VA[2]**	**VA[3]**	**NC**	**SC[1]**	**SC[2]**	**FL[1]**	**FL[2]**	**LA**	**TX**
spotfin mojarra (*Eucinostomus argenteus*)				X			X	X				
spotted hake (*Urophycis regia*)			X									
spotted seatrout *(Cynoscion nebulosus)* *****			X			X		X			X	
striped anchovy (*Anchoa hepsetus*)				X			X	X				
striped bass (*Morone saxatilis*) *****	X	X	X	X	X	X						
striped burrfish (*Chilomycterus schoepfii*)	X							X				
striped killifish (*Fundulus majalis*)								X				
striped mullet (*Mugil cephalus)*							X	X				X
summer flounder (*Paralichthys dentatus*) *****	X		X	X	X	X	X	X				
tautog *(Tautoga onitis)******			X	X								
threadfin shad (*Dorosoma petenense*)								X				
weakfish (*Cynoscion regalis*) *****			X	X	X	X		X				
western mosquitofish (*Gambusia affinis*)								X				
white mullet (*Mugil curema*)							X	X				
white perch (*Morone Americana)*		X		X	X							
white-fin sharksucker (*Echeneis neucratoides*)					X							
winter flounder (*Pseudopleuronectes americanus*) *****	X			X								
<u>Transient Invertebrates</u>												
American grass shrimp (*Periclimenes americanus*)										X		
Atlantic brief squid (*Lolliguncula brevis*)								X				
Bermuda night shrimp (*Processa bermudensis*)										X		
blue crab (*Callinectes sapidus*)	X	X	X	X	X	X	X	X	X	X	X	X
brackish grass shrimp (*Palaemonetes intermedius*)										X		
brown shrimp (*Farfantepenaeus aztecus*)							X	X			X	
daggerblade grass shrimp (*Palaemonetes pugio*)	X	X		X		X	X	X	X	X		X
Florida stone crab (*Menippe mercenaria*)							X		X			
grass shrimp (*Palaemonetes* spp.)					X						X	
iridescent swimming crab (*Portunus gibbesii*)									X			

Transient Invertebrates Continued	**MD[1]**	**MD[2]**	**VA[1]**	**VA[2]**	**VA[3]**	**NC**	**SC[1]**	**SC[2]**	**FL[1]**	**FL[2]**	**LA**	**TX**
lesser blue crab (*Callinectes similis*)							X	X				
longnose spider crab (*Libinia dubia*)									X			
marsh grass shrimp (*Palaemonetes vulgaris*)	X	X		X		X	X	X	X			X
Penaeiod spp.									X			
pink shrimp (*Farfantepenaeus duorarum)*							X	X		X		X
white shrimp (*Litopenaeus setiferus)*							X	X				
Zostera shrimp (*Hippolyte zostericola*)										X		
Total number of species	**21**	**18**	**33**	**40**	**32**	**35**	**43**	**77**	**23**	**29**	**26**	**19**

Location descriptions and citations: MD[1]: Flag Pond, Maryland (Breitburg 1999 and unpublished data); MD[2]: Patuxent River, Maryland (D. Breitburg and T. Miller, unpublished data); VA[1]: Piankatank River, Virginia (Harding and Mann 1999, 2001b); VA[2]: Fisherman's Island, Virginia (Luckenbach et al. 1997, 1998; O'Beirn et al. 1999; Nestlerode 2004); VA[3]: Rappahanock River, Virginia (Luckenbach and Ross 2003)
NC: Neuse River and Pamlico Sound, North Carolina (Lenihan et al. 1998); SC[1]: Inlet Creek and Toler's Cove, South Carolina (Wenner et al. 1996; Coen et al. 1999b, 2006a); SC[2]: North Inlet-Winyah Bay NERR, South Carolina (Dame et al. 2002; D. Allen et al. 2007, and unpublished data from the USC Baruch Field Station's CREEK Project), FL[1]: Southwest Florida (Tolley et al. 2005a, 2005b); FL[2]: Southwest Florida (Glancy et al. 2003, and unpublished data); LA: Barataria Bay, Louisiana (Plunket and La Peyre 2005); TX: West Bay (Zimmerman et al. 1989).

***Species managed by ASMFC as part of fisheries management plans**

Figure 1a. Examples of intertidal and subtidal shellfish habitats. A & B: Pen shell, *Atrina zelandica*, aggregations in New Zealand (Source: Simon Thrush, National Institute of Water and Atmospheric Research, New Zealand); C: *Modiolus modiolus* reefs in St. Joe Bay, Florida (Source: Brad Peterson, State University of New York, Stony Brook); D: Nesting oyster catchers on intertidal shell accumulations along the Intracoastal Waterway (Source: Phil Wilkinson, South Carolina Department of Natural Resources); E: Intertidal oyster reefs at Canaveral National Seashore (Source: Loren Coen, author); F: Close-up of intertidal oysters on South Carolina reefs (Source: Loren Coen, author).

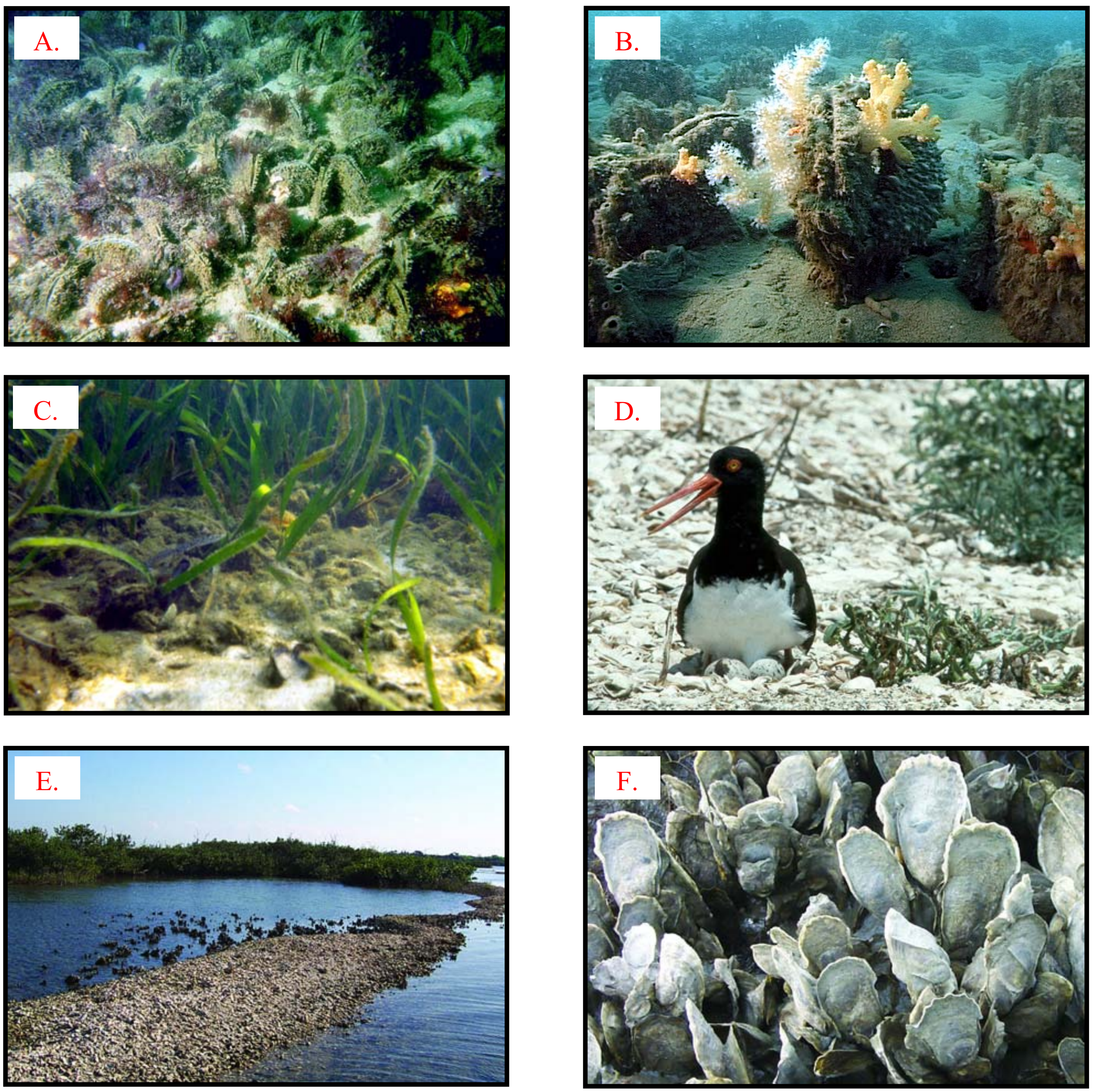

Figure 1b. Examples of intertidal and subtidal shellfish habitats continued. A: *Argopecten irradians* (Source: Janessa Cobb, Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute); B: Underwater shot of *Crassostrea virginica* from a Maryland reef (Source: Ken Paynter, University of Maryland, College Park); C: *Geukensia demissia* amongst *Spartina* stems (Source: Loren Coen, author); D: Mussel accumulations from Louisiana (Source: Earl Melancon, Nicholls State University).

Figure 2. Schematic showing relationship of major oyster reef sampling/remote sensing techniques to spatial resolution (Source: Grizzle et al. 2005).

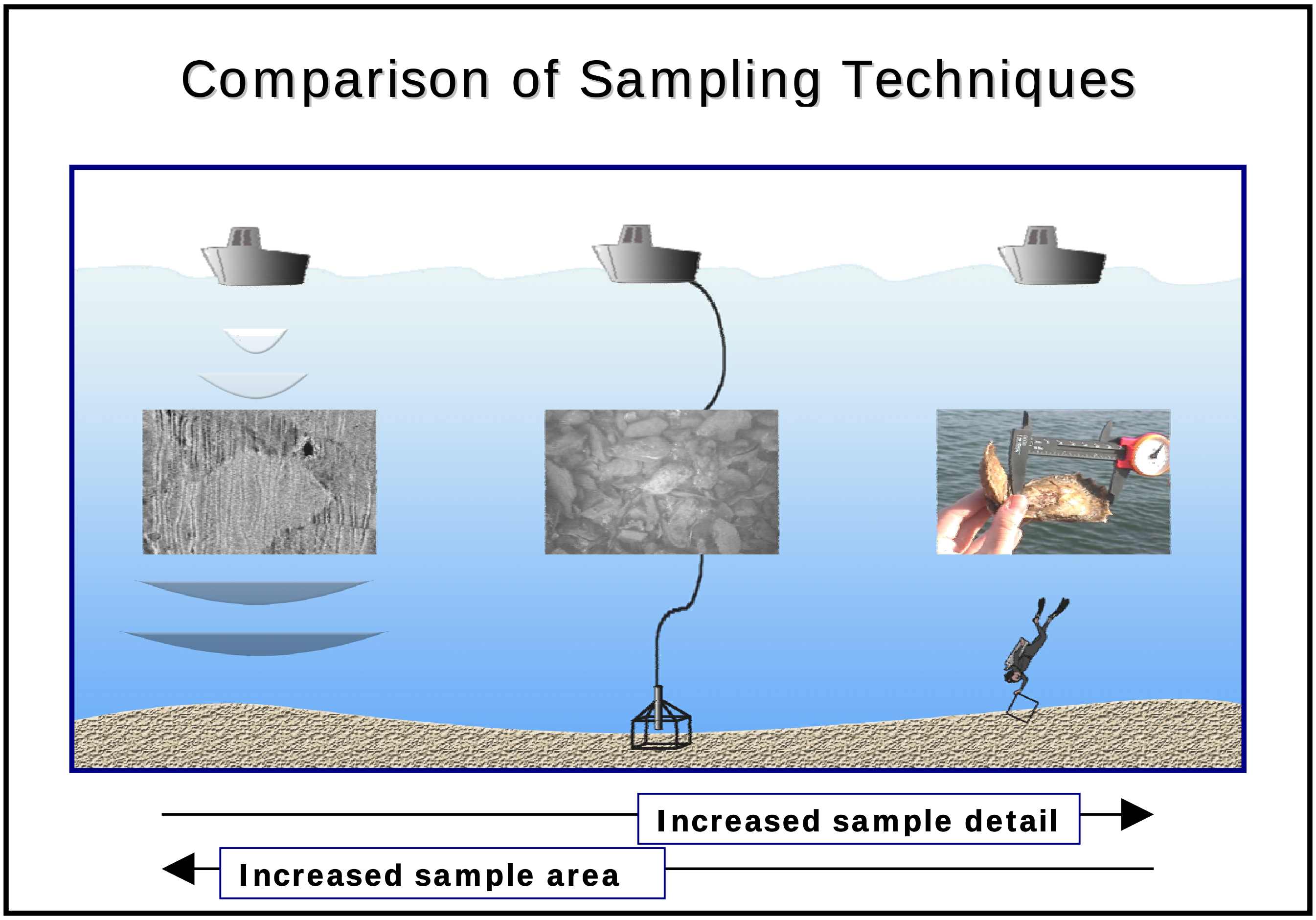

Figure 3. Time series of intertidal oyster reef changes in east-central (Canaveral National Seashore, CANA) Florida. Aerial imagery showing increase in dead reef areas (red) compared to living (green) over time, most probably caused by increased boating activities (Source: Grizzle et al. 2002).

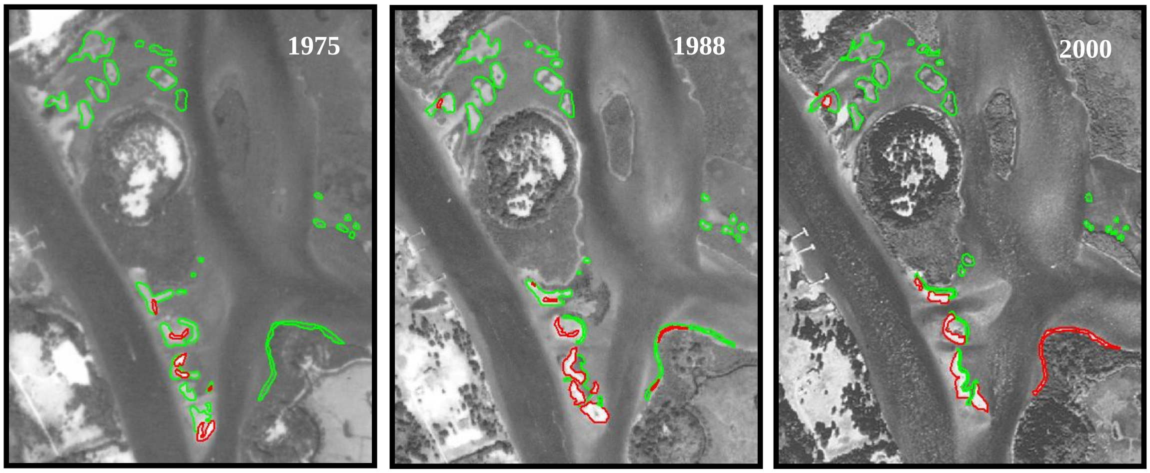

Figure 4. Photos of *Perna viridis* growing with intertidal oysters (*Crassostrea virginica*) on bridge pillings in Tampa Bay, Florida, in 2003 (Source: Loren Coen, author (top), and Jon Fajans, Keys Marine Lab, Long Key, Florida (bottom)). Now that this species has been observed in South Carolina, it remains to be seen what impacts may occur on intertidal oysters reefs and other habitats.

Figure 5. An example of a habitat map for the occurrence of unique reef types along Florida coast (adapted from Jaap and Hallock 1990).
(Available: http://www.nhm.ac.uk/hosted_sites/quekett/Others/Special-reef.html)

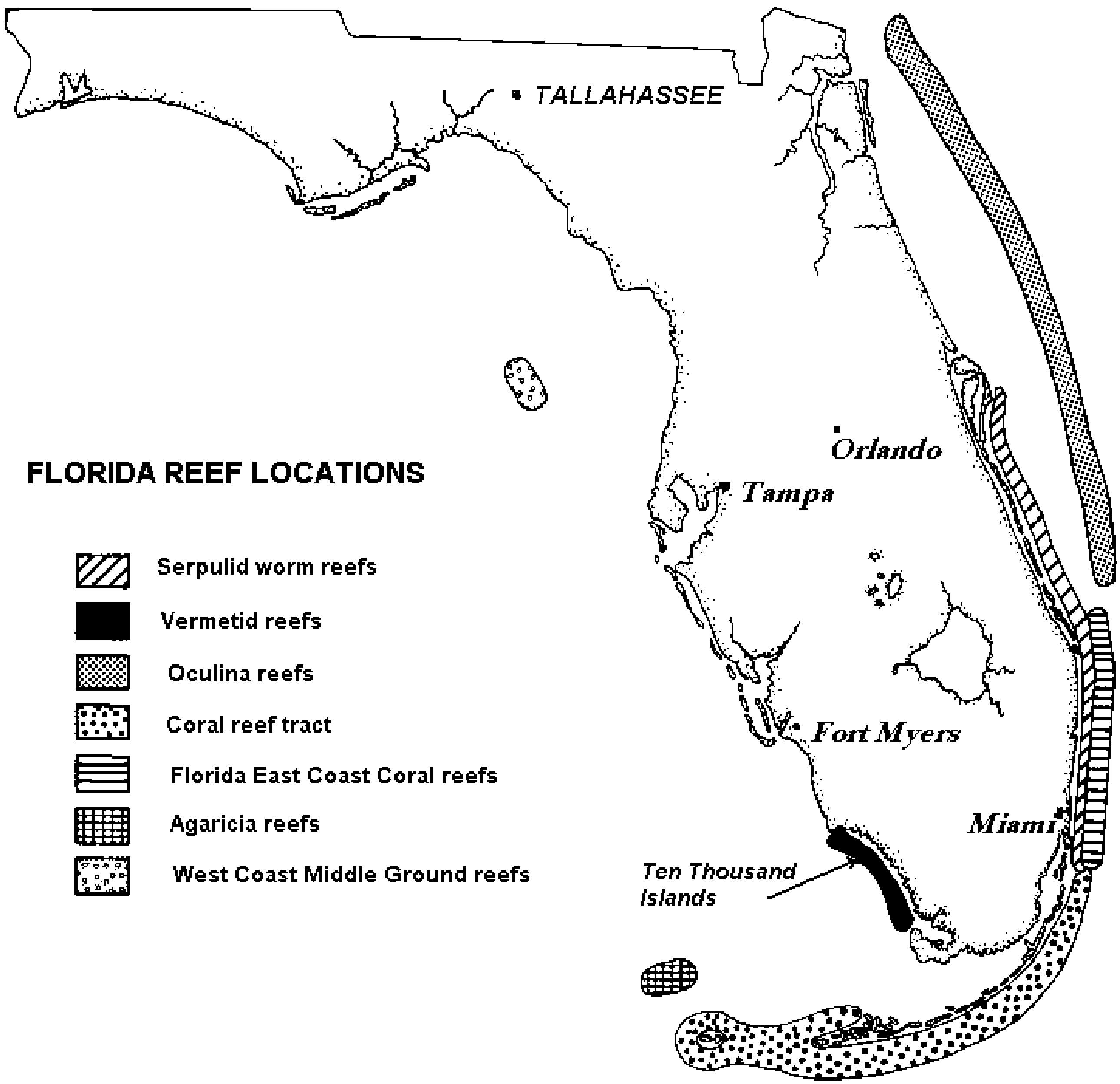

Figure 6. Multispectral aerial image of intertidal oyster reef types in South Carolina. The dotted square on the right indicates intertidal oyster flats and the dashed square on the left indicates fringing oyster reefs adjacent to the marsh. GeoVantage 4 discrete spectral bands (B,G,R,NIR), Ortho-rectified imagery (+3m horizontal accuracy), tuneable bands (10 nm), illumination normalization, 0.25 m spatial resolution. Images were taken at negative low tides only, from May to October, when the marsh was alive and green, the sun angle was restricted to 45^{o} to lower glint, the winds were calm or offshore less than 8 km/h, and no cloud cover was over the intertidal areas. Imagery from Hamlin Creek and Gray Bay, South Carolina.

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