Eastern Oyster
Crassostrea virginica (Gmelin, 1791)

Contributor: Peter Kingsley-Smith (SCDNR)

DESCRIPTION

Taxonomy and Basic Description

The Eastern oyster, *Crassostrea virginica*, was first identified by Gmelin (1791) and over time has been shown to be synonymous with a number of other species. Harry (1985) recognized only 4 species in the genus *Crassostrea*, namely *C. angulata, C. virginica, C. columbiensis, and C. gigas*. Menzel (1987), observing ease of hybridization and chromosomal patterns in hybrids, suggested that *C. virginica*, *C.* columbiensi,s and *C. gigas* should be considered the same species with, *C. columbiensis* and *C. rhizophorae* being subspecies of *C. virginica*. *Crassostrea v. guyensis* and *C. v. lacerate*—reported from Venezuela—are subspecies of *C. virginica* (Ahmed 1975), and *C. crassa*, *C. brasiliana*, and *C. floridensis* are synonyms of *C. virginica* (Abbott 1974; Quayle 1980; Castillo-Rodriguez and García-Cubas 1986). Ahmed (1971, 1975) believed *C. madrasensis* in India and Pakistan to be *C. virginica* based on their very close morphological similarities, while Lamy (1929-1930) reported many other synonyms of *C. virginica* (see also recent papers by Reece et al. 2008, Cordes et al. 2008, and references therein.).

The Eastern oyster, *Crassostrea virginica* (Phylum Mollusca; Class Pelecypoda or Bivalvia; Order Lamellibranchia; Family Ostreidae), is a monomyarian (anterior adductor muscle has been lost) lamellibranch with a pronounced bilateral asymmetry and restricted coelom typical of the class (Seed 1983). The shell of *C. virginica* consists of 2 calcareous valves, joined by a resilient hinge ligament, and serves as an exoskeleton to support the soft internal organs and prevent the collapse of the mantle cavity. The left valve is almost always thicker and heavier than the right valve and more deeply cupped (Yonge 1960; Galtsoff 1964), while the post-settlement form is cemented to the substrate on the left valve. Shell hinge teeth are absent in *C. virginica*, although a buttress on the right valve fits into a depression on the left valve (Stanley and Sellers, 1986). The interior of the shell of *C. virginica* has a purple pigmented adductor muscle scar located slightly posteriorly and ventrally. This feature can be used to distinguish *C. virginica* from other similar species of *Crassostrea* (e.g. lightly pigmented in *C. rhizophorae* and *C. gigas*; unpigmented in *C. rivularis*). A second muscle scar—of the Quenstedt's muscle—is situated ventral to and a short distance from the hinge (Stanley and Sellers 1986). Species of *Crassostrea* are distinguishable from species of *Ostrea* by the promyal chamber which is well-developed in *Crassostrea* but not in *Ostrea*. The growth form of *C. virginica* is highly variable (McLean 1941) and is strongly affected by environmental conditions.

The internal organs of bivalves are covered by a fleshy fold of tissue called the mantle that deposits the shell. The gills of *C. virginica* consist of 4 folds of tissue that are suspended from the visceral mass and occupy much of the mantle cavity. Together with the mantle, the gills are the main organs of respiration and create water currents that enable food particles to be captured and sorted by the labial palps prior to ingestion at the mouth and digestion. Extensive communities of filter-feeding bivalves are capable of improving water clarity and quality through high filtration rates associated with feeding and the transfer of nutrients from the water column to the benthos (Ulanowicz and Tuttle 1992; Dame 1999; Dame et al. 2001; Newell 2004; Porter et al. 2004). The most comprehensive work describing the anatomy and histology of *C. virginica* is that by Galtsoff (1964), with a thorough review of many aspects of the biology and ecology of this species having recently been compiled by Kennedy et al. (1996).

Crassostrea virginica is a protandric, gonochoristic or dioecious alternate hermaphrodite (Coe 1943; Mackie 1984) with an annual reproductive cycle that culminates in spawning and external fertilization in the water column. Reproduction is typically triggered by periods of higher water temperatures (e.g. Loosanoff and Davis 1963) that support abundant phytoplankton that enable larvae to grow rapidly. Adult oysters are responsive to macroscale environmental changes that stimulate gametogenesis and spawning when conditions are suitable for larval survival and gametogenesis. These processes are synchronized between the sexes such that eggs and sperm are released concurrently, maximizing the number of eggs that are successfully fertilized. Following fertilization, blastula and gastrula stages occur, and the first larval form (trochophore) hatches from the egg and begins to swim (Galtsoff 1964). The trochophore persists for 24 to 48 hours, depending on water temperatures, before developing into the veliger (or D-shape) stage which is protected by the larval shell. The planktotrophic veliger stage, which typically lasts 2 to 3 weeks, takes its name from the 'velum'—a structure that enables the veliger to swim and feed and which is resorbed after settlement (Baker and Mann 1994). Temperature and food supply affect the length of the larval period, with increases in time undoubtedly leading to decreased survival due to extended exposure to predators and disease (Underwood and Fairweather 1989). Larvae that survive in the plankton to reach the "eyed" stage explore the substrate as pediveligers, searching for suitable locations to adopt the permanently benthic form whereupon cementation occurs. Early post-settlement and post-metamorphic stages in bivalves are referred to as "spat" which feed, grow, and mature into the adult form.

Status

Crassostrea virginica is not State or Federally listed, although this species plays a pivotal ecological role in the health of marine and estuarine ecosystems as an individual species and collectively as a priority habitat (reef). Populations of *C. virginica*, have declined along much of the Mid-Atlantic coast of the United States during the last century due to a combination of over-harvesting (Gross and Smyth 1946), habitat degradation (Rothschild et al. 1994), reduced water quality (Seliger et al. 1985), disease (Ford and Tripp 1996; Lenihan et al. 1999), the interactions among these factors (Lenihan and Peterson 1998), and ecosystem shifts (see Rothschild et al. 1994; Luckenbach et al. 1999; Dame et al. 2002). Newell (1988) estimated that the extant population of *C. virginica* in Chesapeake Bay was approximately 1% of the biomass present a century earlier. Furthermore, Beck et al. (2009) recently highlighted the imperiled status of shellfish habitats, with an estimated 85% loss of habitat on a global scale, placing them as the most threatened of marine habitats. Wild populations of *C. virginica* are harvested both commercially and recreationally in South Carolina, and aquaculture on leased grounds (culture and mariculture permit areas) is increasing. To ensure that populations of *C. virginica* in South Carolina remain abundant, extensive efforts at the SCDNR Marine Resources Division—both by the Office of Fisheries Management and the Marine Resources Research Institute Shellfish Research Section—continue to be directed towards assessments of the distribution of *C. virginica* statewide to monitor changes in the acreage and condition of intertidal oyster reef habitat using ground-, boat-, and helicopter-based survey techniques.

POPULATION SIZE AND DISTRIBUTION

The Eastern oyster, *Crassostrea virginica* is distributed in the Western Atlantic along the coasts of Brazil and Argentina northwards through the Caribbean and Gulf of Mexico to the St. Lawrence River estuary in eastern Canada, representing a range of some 8,000 km (4,971 mi.) (Buroker 1983; Newball and Carriker 1983; García-Cubas et al. 1987; Andrews 1991). *Crassostrea virginica* has also been introduced to a wide geographic range of localities, including the west coast of North America, Hawaii, Australia, England, Japan, and possibly other areas, but in general has not become established there (Quayle 1988; Arakawa 1990). A review of non-native oyster introductions and the ecological consequences and restoration implications of these actions was recently provided by Ruesink et al. (2005).

HABITAT AND NATURAL COMMUNITY REQUIREMENTS

Crassostrea virginica is critically dependent on a mixture of saltwater with freshwater from land drainage (Butler 1954) and therefore occurs commonly in estuaries and coastal areas of reduced salinity as extensive reefs on hard to firm bottoms, both intertidally and subtidally (Meyer and Townsend 2000; Wilson et al. 2005). *Crassostrea virginica* forms extensive, 3-dimensional reef habitat through the settlement of competent larvae on the shells of previous generations. The natural environmental factors governing the distribution of *Crassostrea virginica* were recently reviewed by Shumway (1996). Adult *C. virginica* are highly tolerant of broad ranges in salinity and temperature, making them well-suited to life in the estuary and, in South Carolina, to a predominantly intertidal distribution. Adult oysters are found in waters where the annual temperature range is from -2°C to 36°C (28-97°F) (Butler 1954; Gunter 1954; Galtsoff 1964). Galtsoff (1964) reported that oysters can survive intertidal temperatures of 46°C to 49°C (115-120°F) when exposed at low tide. In terms of salinity, across its geographic range, *C. virginica* occurs from ~ 5 ppt to ~40 ppt (Galtsoff 1964; Wallace 1966). If left undisturbed in an optimal environment, oysters will continue to grow for many years. Galtsoff (1964), for example, reported a maximal shell height of *Crassostrea virginica* of 36 cm (14 in.), although the majority of oysters experience mortality prior to reaching this size.

More than 95% (over 850 ha or 2,100 acres) of the South Carolina oyster populations are intertidal (Bahr and Lanier 1981; Burrell 1986), consisting of 3-dimensional, multi-generational, vertical clusters of oysters. The vertical height of oyster reefs in an otherwise 2-dimensional sedimentary landscape and the interstitial space generated by these clusters are central to the ecosystem services that they support. Historically, both intertidal and subtidal populations of *C. virginica* were distributed widely throughout coastal South Carolina; however, reported landings of subtidal populations of *C. virginica* have seen a steep decline since the mid-1900s. Anecdotal information from SCDNR shellfish managers and commercial growers indicates that certain estuaries still support limited subtidal populations of *C. virginica*. However, a targeted habitat survey of subtidal oysters in South Carolina has not been undertaken in nearly 45 years (Keith and Cochran 1968).

Intertidal *C. virginica* populations, unlike subtidal populations, form natural breakwaters that protect fringing salt marshes from erosion (e.g. Meyer et al. 1997; Coen and Luckenbach 2000; Piazza et al. 2005). South Carolina has more acreage of salt marsh (234,058 ha or 578,368 acres, Newell and Pearson 2009) than any other Atlantic Coast state, and much of it is protected by adjacent intertidal oyster reefs. Many of the species utilizing these habitats take advantage of their close proximity to one another as both nursery and foraging grounds.

CHALLENGES

Salinity affects the distribution of oysters directly through its physiological consequences on the oysters themselves and indirectly through its role in determining the relative incidence of predators (e.g. fish, gastropods, crabs, and polyclad flatworms), pests (e.g. boring sponges, mud worms, pea crabs), competitors (e.g. barnacles, sponges, bryozoans, and other molluscs), and disease-causing protistan parasites, in particular those responsible for the endemic diseases MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*). These challenges to oyster populations generally increase at higher salinities.

Crassostrea virginica has been heavily exploited and widely cultivated throughout much of its geographic range (Galtsoff, 1964; García-Cubas et al. 1987; Quayle and Newkirk 1989; Andrews 1991; Menzel 1991; Nascimento 1991). Sustainable management of state and public shellfish grounds and Best Management Practice (BMP) approaches to aquaculture, are therefore important for the long-term viability of *C. virginica* populations in South Carolina. Although *C. virginica* in South Carolina has not been as extensively exploited as the *C. virginica* populations in the Mid-Atlantic States, the rapid pace of coastal development has created numerous threats to tidal creek habitats with inevitable undesirable impacts (e.g. Lerberg et al. 2000; Van Dolah et al. 2004; Holland et al. 2004). Particularly, these involve: increased runoff from upland clearing and associated non-pervious surfaces; contaminants (which are particularly detrimental to larval stages) such as pesticides and heavy metals (see Capuzzo 1996 and Roesijadi 1996, respectively, for recent reviews); water quality closures resulting in concentrated harvest pressure on open, harvestable beds; impacts from dredging and other channel manipulations; and boat-related impacts. Boat wakes and intense harvesting can both easily damage intertidal reefs, and the vegetated marsh habitats protected by these reefs can rapidly erode when the reefs are compromised (e.g. Kennish 2002). Furthermore, several South Carolina estuaries including Charleston Harbor, Winyah Bay, and Port Royal Sound have been heavily impacted by industrial activities, shipping, chronic pollution, and habitat destruction related to urbanization. These threats to oyster reefs have prompted extensive efforts to protect, restore, and enhance these critical coastal habitats.

CONSERVATION ACCOMPLISHMENTS

Oyster reefs are now broadly recognized as “ecosystem engineers” (see Luckenbach et al. 1999; Gutiérrez et al. 2003; ASMFC 2007) that form complex habitats utilized by numerous finfish, invertebrates, wading birds, and mammals (Coen et al. 1999; Lehnert and Allen 2002; ASMFC

2007; Peterson et al. 2003; Shervette and Gelwick 2007, 2008). Within the Southeast Region, the South Atlantic Fishery Management Council (SAFMC) has designated estuarine marshes, oyster reefs, associated estuarine water columns, intertidal flats, and areas of submerged aquatic vegetation (SAV) as essential fish habitat (EFH). In South Carolina, oyster reefs are also considered critical habitats of concern in both the State Conservation Plan and the State Wildlife Action Plan (formerly the CWCP), primarily due to their provision of habitat for a number of species of concern (e.g. Atlantic blue crab, *Callinectes sapidus*; stone crab, *Menippe mercenaria*; Southern Flounder, *Paralichthys lethostigma*; and the American oystercatcher, *Haematopus palliates*). Both the ACE Basin National Estuarine Research Reserve (NERR) and the North Inlet-Winyah Bay NERR list oyster reefs as important habitat, and The Nature Conservancy recently completed a biological assessment of the Carolinian Ecoregion that specifically identified oyster reefs as a priority conservation target (DeBlieu et al. 2005).

Oyster reefs provide essential habitat for federally-managed (ASMFC) species such as Red Drum (*Sciaenops ocellatus*), Atlantic Croaker (*Micropogonias undulatus*), Black Sea Bass (*Pogonias cromis*), Spotted Sea Trout (*Cynoscion nebulosus*), Spot (*Leiostomus xanthurus*), Atlantic Menhaden (*Brevoortia tyrannus*), Southern Flounder (*Paralichthys lethostigma*), members of the snapper-grouper complex (managed by SAFMC), Atlantic blue crab (*Callinectes sapidus*), and penaeid shrimp species (Shervette and Gelwick 2007, 2008). A number of prey species of the Southern Flounder, *P. lethostigma*, a South Carolina priority species in the SWAP, for example, have been shown to be associated with edge habitats including oyster reefs (Reagan 1985). Many of these species depend on the inter-relationships of oyster reefs and adjacent marsh habitats for their survival during various life stages. In turn, these species provide prey for SAFMC-managed species such as Spanish Mackerel (*Scomberomorus maculatus*), King Mackerel (*Scomberomorus cavalla*), and Cobia (*Rachycentron canadum*), as well as NOAA Fisheries-managed highly migratory species (HMS) such as sharks and billfishes.

Numerous species prey directly on oysters, including xanthid crabs, such as the stone crab, *M. mercenaria* and the Atlantic mud crab, *Panopeus herbstii* (Tolley and Volety 2005), both species of concern in SC. In turn, several finfish species, including the Naked Goby (*Gobiosoma bosc*) and the Striped Blenny (*Chasmodes bosquianus*), are known to feed on these xanthid crabs, generating trophic complexity and the potential for the formation of trophic cascades (Grabowski 2004). Mann and Harding (1998) investigated the trophic interactions among oysters, fishes, and benthic predators on restored oyster reefs and showed that small and intermediate sized fishes such as gobies (e.g. Seaboard Goby, *Gobiosoma ginsburgi* and *G. bosc*) and blennies (e.g. Feather Blenny *Hypsoblennius hentz* and *C. bosquianus*), were abundant in Chesapeake Bay oyster reef-dominated ecosystems. The presence of these species on reef structures is thought to attract larger pelagic predatory species such as Striped Bass (*Morone saxatilis*), Bluefish (*Pomatomus saltatrix*), Weakfish (*Cynoscion regalis*), Southern Flounder (*P. lethostigma*), Sheepshead (*Archosargus probatocephalus*), and Spotted Seatrout (*C. nebulosus*). Other benthic predators, such as the Atlantic blue crab (*C. sapidus*)—another South Carolina priority species for conservation—have also been shown to be strongly associated with *C. virginica* reefs (Mann and Harding 1998).

Several studies have shown that the 3-dimensional structure of oyster reefs attracts greater numbers of resident and transient nektonic species than sand- or mud-bottom habitats (Posey et al. 1999; Harding and Mann 2001; Lenihan et al. 2001; Plunket and Peyre 2005; Coen et al. 2007; Kingsley-Smith et al. 2013). Breitburg (1999) defined 3 groups of nekton associated with subtidal *C. virginica* reefs in the Chesapeake Bay: (1) reef residents whose primary habitat is the reef; (2) facultative residents generally associated with structured habitats; and (3) transient species which forage on or near the reef but are wide-ranging. Furthermore, a number of oyster reef resident fishes—including *G. bosc*, *C. bosquianus*, *H. hentz*, Freckled Blenny (*Hypsoblennius ionthas*), Skilletfish (*Gobiesox strumosus*), Oyster Toadfish *Opsanus tau,* and Gulf Toadfish (*O. beta*) have been shown to be dependent on oysters for reproduction, depositing their eggs on or inside oyster shells (Breitburg 1999; Coen et al. 1999). In summary, it appears that the diverse range of organisms associated with oyster reefs creates complex food webs that sustain higher trophic levels than surrounding sediment or marsh habitats (Wrast 2008; Quan et al. 2012). Additionally, oyster reefs serve as critical foraging habitat for the American Oystercatcher, *Haematopus palliatus* (a Species of Concern of Highest Priority) and other shorebirds such as egrets, herons, sandpipers, plovers, and godwits, all of which are listed in the South Carolina SWAP as species of highest priority. The largest concentration of overwintering *H. palliatus* occurs in South Carolina, utilizing oyster reefs as foraging grounds (Tomkins 1947; Sprunt and Chamberlain 1949; Nol et al. 2000). A recent study by Sanders et al. (2004) also highlighted the importance of washed shell rakes as roosting sites for *H. palliatus*.

In recognition of the value of oyster reefs as critical habitats, considerable efforts have been made to successfully secure Federal funding in support of research and community-based restoration and enhancement projects utilizing a variety of traditional (bagged and loose oyster shell) and alternative materials (e.g. oyster castle, revitalized abandoned and unwanted crab traps) to increase the availability of oyster reefs as habitat for a diverse array of associated fauna including a number of high priority conservation species. Furthermore, as protection for existing *C. virginica* populations, the South Carolina Department of Natural Resources regulates the importation of oysters for placements in its State waters, primarily for mariculture, requiring inspections for the presence of "hitch-hiker species" upon arrival in the State and restricting importation from areas of known diseases (such as Dermo and MSX). Disease testing is required prior to importation, with zero tolerance for the presence of known diseases. Hatchery certification is also available to permit the importation of oyster seed from other states, provided a number of criteria, protocols, and procedures related to water quality and disease are satisfied.

CONSERVATION RECOMMENDATIONS

- Apply both traditional and alternative approaches to oyster reef habitat restoration and enhancement activities, and engage the community in conservation and stewardship through volunteer opportunities.
- Conduct scientifically rigorous monitoring to evaluate the habitat value of oyster reefs to conservation priority species as well as commercially, recreationally, and ecologically-important species of finfish, invertebrates, and birds.
- Regularly update importation policies for cultured oysters to reflect changes in threats to native oysters and to make the best use of all available information and technology.
- Regulate recreational and commercial harvesting of wild oyster populations and mariculture activities in collaboration with SCDHEC in order to ensure sustainable harvesting and to protect human health.

- Monitor the population status of oysters statewide using on-the-ground efforts, aerial surveys (including helicopter-based imagery capture), and GIS applications.
- Collaborate with the South Carolina Algal Ecology Laboratory (SCAEL) to investigate the causes of harmful algal blooms and their interactions with oyster populations.
- Collaborate with the appropriate agencies and municipalities to improve and implement Best Management Practices in terms of responsible urban planning to minimize and mitigate the effects of terrestrial freshwater inputs on oyster populations.

MEASURES OF SUCCESS

Determining that populations of *C. virginica* in South Carolina are remaining stable through the collection of annual fishery statistics and population monitoring would constitute a measure of success. An absence of human health problems would also be a measure of success in demonstrating the effectiveness of the collaborative resource management implemented by the SCDNR and SCDHEC. Continued monitoring of the fauna associated with natural, restored, and enhanced reef habitats—and in particular demonstrating their value to priority conservation species—would also be a measure of success.

LITERATURE CITED

Abbott, R.T. (1974). *American seashells. The Marine Mollusca of the Atlantic and Pacific Coasts of North America, 2nd Edition*. Van Nostrand Reinhold, New York. 663 pp.

Ahmed, M. (1971). Oyster species of West Pakistan. *Pakistan J. Zool.* 3:229-236.

Ahmed, M. (1975). Speciation in living oysters. *Adv. Mar. Biol.* 13:357-397.

Andrews, J.D. (1991). The oyster fishery of eastern North America based on *Crassostrea virginica*. *In*: W. Menzel (ed.), *Estuarine and Marine Bivalve Mollusk Culture*. CRC Press, Boston, pp. 11-23.

Arakawa, K.Y. (1990). Commercially important species of oysters in the world. *Mar. Behav. Physiol.* 17:1-3.

ASMFC (2007). *The importance of habitat created by shellfish and shell beds along the Atlantic Coast of the U.S.* Prepared by L.D. Coen & R. Grizzle with contributions by J. Lowery & K.T. Paynter Jr. 108 pp.

Bahr, L.M. & Lanier, W.P. (1981). The ecology of intertidal oyster reefs of the South Atlantic Coast: a community profile. *U.S. Fish Wildl. Serv. Program FWS/OBS/ -81/15*. 105 pp.

Baker, S.M. & Mann, R. (1994). Description of metamorphic phases in the oyster *Crassostrea virginica* and effects of hypoxia on metamorphosis. *Mar. Ecol. Prog. Ser.* 104:91-99.

Beck, M.B., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M., Lenihan, H., Luckenbach, M.W., Toropova, C.L. & Zhang, G. (2009). *Shellfish Reefs at Risk: A Global Analysis of Problems and Solutions*. The Nature Conservancy, Arlington VA. 52 pp.

Breitburg, D.C. (1999). Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? *In*: M.W. Luckenbach, R. Mann & J.A. Wesson, (eds), *Oyster reef habitat restoration: A synopsis and synthesis of approaches.* Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 239-250.

Buroker, N.E. (1983). Population genetics of the American oyster, *Crassostrea virginica* along the Atlantic coast and Gulf of Mexico. *Mar. Biol.* 75:99-112.

Burrell, V.G. Jr. (1986). Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) – American oyster. *U.S. Fish Wildl. Serv. Biol. Rep.* 82 (11.57), U.S. Army Corps of Engineers TR EL-82-4. 17 pp.

Butler, P.A. (1954). Summary of our knowledge of the oyster in the Gulf of Mexico. *Fish. Bull.* 55:479-489.

Capuzzo, J.M. (1996). The bioaccumulation and biological effects of lipophilic organic contaminants (Chapter 15). *In*: Kennedy, V.S., Newell, R.I.E. & Eble, A.F. (eds), *The Eastern oyster,* Crassostrea virginica. Maryland Sea Grant College, University of Maryland System, College Park, Maryland, pp. 539-557.

Castillo-Rodríguez, A.G. & García-Cubas, A. (1986). Taxonomía y anatomía comparada de las ostras en las costas de México. *An. Inst. Cienc. Mar. Limnol., Univ. Natl. Auton. México* 13:249-314.

Coe, W.R. (1943). Sexual differentiation in mollusks. I. Pelecypods. *Quart. Rev. Biol.* 18:154-164.

Coen, L.D. & Luckenbach, M.W. (2000). Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation. *Ecol. Eng.* 15:323-343.

Coen, L.D., Luckenbach, M.W. & Breitburg, D.L. (1999). The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. *In*: L. R. Benaka, (ed.), *Fish Habitat: Essential Fish Habitat and Rehabilitation*. Amer. Fish. Soc., Symp. 22, Bethesda, MD, pp. 438-454.

Coen, L., Walters, K., Wilber, D. & Hadley, H. (2007). A South Carolina Sea Grant report of a 2004 workshop to examine and evaluate oyster restoration metrics to assess ecological function, sustainability and success: results and related information. 24 pp. plus appendices.

Cordes, J.F., Xiao, J. & Reece, K.S. (2008). Discrimination of oyster species (*Crassostrea*: Mollusca) based on restriction fragment length polymorphism (RFLP) analysis of nuclear and mitochondrial DNA markers. *J. Shellfish Res.* 27:1155-1161.

Dame, R.F. (1999). Oyster reefs as components in estuarine nutrient cycling: Incidental or controlling? *In*: Luckenbach, M.W., Mann, R. & Wesson, J.A. (eds), *Oyster reef habitat restoration: a synopsis and synthesis of approaches.* Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 267–280.

Dame, R., Bushek, D. & Prins, T. (2001). Benthic suspension feeders as determinants of ecosystem structure and function in shallow coastal waters. *Ecol. Stud.* 151:11-37.

Dame R.F., Bushek, D., Allen, D., Lewitus, A.J., Edwards, D., Koepfler, E. & Gregory, L. (2002). Ecosystem response to bivalve density reduction: management implications. *Aquat. Ecol.* 36:51–65.

DeBlieu, J., Beck, M., Dorfman, D. & Ertel, P. (2005). Conservation in the Carolinian ecoregion: an ecoregional assessment. The Nature Conservancy, Arlington, VA.

Ford, S.E. & Tripp, M.R. (1996). Diseases and defense mechanisms. *In*: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (eds), *The Eastern oyster,* Crassostrea virginica. Maryland Sea Grant, College Park, MD, pp. 581-660.

Galtsoff. P.S. (1964). The American oyster, *Crassostrea virginica* Gmelin. *U.S. Fish. Wildl. Serv. Fish. Bull.* 64.

García-Cubas, A., Castillo-Rodríguez, Z.G., Alvarez-Herrera, A. & Muñoz-Chagin, R. (1987). Moluscos comestibles en las costas de México. Memorias III, Reunion Malacología Conquiliologia. *Soc. Méx. Malacol. Conquil., Univ. Natl. Auton*. México, Monterey, Nuevo Leon, pp. 429-456.

Grabowski, J.H. (2004). Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995-1004.

Gross, F. & Smyth, J.C. (1946). The decline of oyster populations. *Nature* 157:540-542.

Gunter, G. (1954). The problem in oyster taxonomy. *Syst. Zool.* 3:134-137.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L. & Iribarne, O.O. (2003). Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101:79-90.

Harding, J.M. & Mann, R. (2001). Diet and habitat use by bluefish, *Pomatomus saltatrix*, in a Chesapeake Bay estuary. *Environ. Biol. Fish.* 60:401-409.

Harry, H.W. (1985). Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). *Veliger* 28:121-158.

Holland, F., Sanger, D., Gawle, C.P., Lerberg, S.B., Santiago, M.S., Riekerk, G.H.M. & Zimmerman, L.E. (2004). Linkages between tidal creek ecosystems and the landscape and demographic attributes of their watersheds. *J. Exp. Mar. Biol. Ecol.* 298:151-178.

Keith, W.J. & Cochran, H.S. Jr. (1968). Charting of subtidal oyster beds and experimental planting of seed oysters in South Carolina. Bears Bluff Laboratories, Wadmalaw Island, South Carolina Contribution No. 48. 19 pp.

Kennedy, V.S., Newell, R.I.E. & Eble, A.F. (eds) (1996). *The Eastern oyster,* Crassostrea virginica. Maryland Sea Grant College, University of Maryland System, College Park, Maryland.

Kennish, M.J. (2002). Impacts of motorized watercraft on shallow estuarine and coastal marine environments. *J. Coastal Res. Special Issue* No. 37:1-202.

Kingsley-Smith, P.R., Joyce, R.E., Arnott, S.A., Roumillat, W.A., McDonough, C.J. & Reichert, M.J.M. (2012). Habitat use of intertidal Eastern oyster (*Crassostrea virginica*) reefs by nekton in South Carolina estuaries. *J. Shellfish Res*. 31(4):1009-1021.

Lamy, E. (1929-1930). Révision des *Ostrea* vivants du Muséum National d'Histoire Naturelle de Paris. *J. Conchiol.* 73(1):1-46, (2):71-108, (3):133-168, (4):233-275.

Lehnert, R.L. & Allen, D.M. (2002). Nekton use of subtidal oyster shell habitat in a southeastern U.S. estuary. *Estuaries* 25:1015-1024.

Lenihan, H.S., Micheli, F., Shelton, S.W. & Peterson, C.H. (1999). The influence of multiple environmental stressors on susceptibility to parasites: an experimental determination with oysters. *Limnol. Oceanogr.* 44:910-924.

Lenihan, H.S. & Peterson, C.H. (1998). How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol. Appl*. 8:128-140.

Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W. & Colby, D.R. (2001). Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecol. Appl*. 11:764-782.

Lerberg, S.B., Holland, A.F. & Sanger, D.M. (2000). Responses of tidal creek macrobenthic communities to the effects of watershed development. *Estuaries* 23:838-853.

Loosanoff, V.L. & Davis, H.C. (1963). Rearing of bivalve molluscs. *Adv. Mar. Biol.* 1:1-136.

Luckenbach, M.W., Mann, R. & Wesson, J.A. (eds.) (1999*). Oyster reef habitat restoration: a synopsis and synthesis of approaches.* Virginia Institute of Marine Science Press, Gloucester Point, VA, 358 pp.

Mackie, G. (1984). *Bivalves*. *In*: Tompa, A.S., Verdonk, N.H. & van den Biggelaar (eds), *The Mollusca, Volume 7*. Academic Press, New York. pp. 351-418.

Mann, R. & Harding, J.M. (1998). Continuing trophic studies on constructed "restored" oyster reefs. Annual research report to the U.S. Environmental Protection Agency, Chesapeake Bay Program, Living Resources Committee, Virginia Institute of Marine Science, Gloucester Point, VA. 71 pp.

McLean, R.A. (1941). The oysters of the Western Atlantic. *Notulae Naturae, Acad. Nat Sci. Phila*. No. 67. 14 pp.

Menzel, R.W. (1987). Hybridization of oysters and clams. *In*: Tiews, K. (ed.). *Selection, hybridization, and genetic engineering in aquaculture.* Proc. World Symp., Bordeau, May 27-30, 1986, Vol. II, Berlin, pp. 47-59.

Menzel, R.W. (1991). Cultural practices and production of the American oyster, with emphasis on the south Atlantic and Gulf of Mexico. *In*: Menzel, W. (ed.), *Estuarine and marine bivalve mollusk culture*, CRC Press, Boston, pp. 25-34.

Meyer, D.L. & Townsend, E.D. (2000). Faunal utilization of created intertidal Eastern oyster (*Crassostrea virginica*) reefs in the southeastern United States. *Estuaries* 23:34-45.

Meyer, D.L., Townsend, E.C. & Thayer, G.W. (1997). Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restor. Ecol.* 5:93-99.

Nascimento, I.A. (1991). *Crassostrea rhizophorae* (Guilding) and *C. brasiliana* (Lamarck) in South and Central America. *In*: Menzel, W. (ed.), *Estuarine and marine bivalve mollusk culture*, CRC Press, Boston, pp. 125-134.

Newball, S. & Carriker, M.R. (1983). Systematic relationship of the oysters *Crassostrea rhizophorae* and *C. virginica*: a comparative ultrastructural study of the valves. *Amer. Malacol. Bull.* 1:35-42.

Newell, R.I.E. (1988). Ecological changes in Chesapeake Bay: are they the result of over-harvesting the American oyster, *Crassostrea virginica*? *In*: Lynch, M.P., Chrome, E.C. (eds), *Understanding the estuary: advances in Chesapeake Bay research*. Proceedings of a Conference. Chesapeake Bay Research Consortium Publication 129. Baltimore, MD, pp. 536-546.

Newell, R.I.E. (2004). Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J. Shellfish Res.* 23:51-61.

Newell, C.L. & Pearson, M.P. (2009). 2008 shellfish growing area status report, including classification trends for report years 1986 through 2008. SCDHEC Shellfish Sanitation Section, Water Monitoring, Assessment and Protection Division, Environmental Quality Control – Bureau of Water, 2600 Bull Street, Columbia, SC. 10 pp.

Nol, E., Truitt, B., Allen, D., Winn, B. & Murphy, T. (2000). Size of the American oystercatcher population in the United States: Results of the 1999 survey for wintering American oystercatchers: Georgia to Virginia. *Unpublished report*.

Peterson, C.H., Grabowski, J.H. & Powers S.P. (2003). Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar. Ecol. Prog. Ser*. 264:249-264.

Piazza, B.P., Banks, P.D. & LaPeyre, M.K. (2005). The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. *Restor. Ecol*. 13: 499-506.

Plunket, J.T. & La Peyre, M.K. (2005). Comparison of finfish assemblages at clutched shell bottoms and mud bottoms in Barataria Bay, LA. *Bull. Mar. Sci.* 77:155-164.

Porter, E.T., Cornwell, J.C., Sanford, L.P. & Newell, R.I.E. (2004). Effect of oysters *Crassostrea virginica* and bottom shear velocity on benthic-pelagic coupling and estuarine water quality. *Mar. Ecol. Prog. Ser*. 271:61-75.

Posey, M.H., Alphin, T.D., Powell, C.M. & Townsend, E. (1999). Oyster reefs as habitat for fish and decapods. *In*: M. W. Luckenbach, R. Mann & J. A. Wesson, (eds), *Oyster reef habitat restoration: a synopsis and synthesis of approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 229-237.

Quan, W.-M., Humphries, A.T., Shi, L.-Y. & Chen, Y.-Q. (2012). Determination of trophic transfer at a created intertidal oyster (*Crassostrea ariakensis*) reef in the Yangtze River estuary using stable isotope analyses. *Estuar. Coasts*. 35:109-120.

Quayle, D.B. (1980). Tropical oysters: culture and methods. *Internat. Develop. Res. Centre*, Ottawa, Canada, IDRC-TS17e, 80 pp.

Quayle, D.B. (1988). Pacific oyster culture in British Columbia. *Can. Bull. Fish. Aquatic Sci.* 218:1-241.

Quayle, D.B. & Newkirk, G.F. (1989). Farming bivalve molluscs: methods for study and development. *Adv. World Aquaculture* 1:1-294.

Reagan, R.E. (1985). Species profiles: life histories and environmental requirements (Gulf of Mexico) – red drum. *U.S. Fish Wildl. Serv. Div. Biol. Sci.* FWS/OBS-82/11.36. U.S. Army Corps of Engineers, TR EL-82-4. 16 pp.

Reece, K.S., Cordes, J., Stubbs, J.B., Hudson, K.L. & Francis, E.A. (2008). Molecular phylogenies help resolve taxonomic confusion with Asian *Crassostrea* oyster species. *Mar. Biol.* 153:709-721.

Roesijadi, G. (1996). Environmental factors: responses to metals (Chapter 14). *In*: Kennedy, V.S., Newell, R.I.E. & Eble, A.F. (eds), *The Eastern oyster*, Crassostrea virginica. Maryland Sea Grant College, University of Maryland System, College Park, Maryland, pp. 515-537.

Rothschild, B.J., Ault, J.S., Goulletquer, P. & Héral, M. (1994). Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Mar. Ecol. Prog. Ser*. 111:29-39.

Ruesink, J.L., Lenihan, H.S., Trimble, A.C., Heiman, K.W., Micheli, F., Byers, J.E. & Kay, M.C. (2005). Introduction of non-native oysters: ecosystem effects and restoration implications. *Annu. Rev. Ecol. Evol. Syst.* 36:643-689.

Sanders, F.J., Murphy, T.M. & Spinks, M.D. (2004). Winter abundance of the American oystercatcher in South Carolina. *Waterbirds: The International Journal of Waterbird Biology*. 27:83-88.

Seed, R. (1983). Structural organization, adaptive radiation, and classification of molluscs. *In*: Hochachka, P. (ed.), *The Mollusca, Vol. 1*. Academic Press, San Diego, pp. 1-54.

Seliger, H.H., Boggs, J.A. & Biggeley, W.H. (1985). Catastrophic anoxia in the Chesapeake Bay in 1984. *Science* 228:70-73.

Shervette, V.R. & Gelwick, F. (2007). Habitat-specific growth in juvenile pinfish. *Trans. Am. Fish. Soc*. 136:445-451.

Shervette, V.R. & Gelwick, F. (2008). Relative nursery function of oyster, vegetated marsh edge and non-vegetated bottom habitats for juvenile white shrimp, *Litopenaeus setiferus*. *Wetl. Ecol. Manage.* 16:405-419.

Shumway (1996). Natural environmental factors (Chapter 3). *In*: Kennedy, V.S., Newell, R.I.E. & Eble, A.F. (eds), *The Eastern oyster*, Crassostrea virginica. Maryland Sea Grant College, University of Maryland System, College Park, Maryland, pp. 467-513.

Sprunt, A.E. & Chamberlain, E.B. (1949). *South Carolina Bird Life*. University of South Carolina Press. Columbia.

Stanley, J.G., and M.A. Sellers. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico)--American oyster. *U.S. Fish Wildl. Serv. Biol. Rep.* 82(11.64). U.S. Army Corps of Engineers, TR EL-82-4. 25 pp.

Tolley, S.G. & Volety, A.K. (2005). The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. *J. Shellfish Res.* 24:1007-1012.

Tomkins, I.R. (1947). The oystercatcher of the Atlantic Coast of North America and its relation to oysters. *Wilson Bulletin* 59:204-208.

Ulanowicz, R.E. & Tuttle, J.H. (1992). The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. *Estuaries* 15:298-306.

Underwood, A.J. & Fairweather, P.G. (1989). Supply-side ecology and benthic marine assemblages. *Trends Ecol. Evol.* 4:16-20.

Van Dolah, R.F., Jutte, P.C., Riekerk, G.H.M., Levisen, M.V., Crowe, S.E., Lewitus, A.J., Chestnut, D.E., McDermott, W., Bearden, D. & Fulton, M.H. (2004). The condition of South Carolina's estuarine and coastal habitats during 2001-2002: Technical Report. SCDNR – Marine Resources Research Institute. 70 pp.

Wallace, D.H. (1966). Oysters in the estuarine environment. A symposium of estuarine fisheries. *Amer. Fish. Soc., Spec. Publ.* 3:68-73.

Wilson, C., Scotto, L., Scarpa, J., Volety, A., Larramore, S. & Haunert, D. (2005). Survey of water quality, oyster reproduction and oyster health status in the St. Lucie Estuary. *J. Shellfish Res.* 24:157-165.

Wrast, J.L. (2008). Spatiotemporal and habitat-mediated food web dynamics in Lavaca Bay, Texas. M.S. Thesis. Department of Life Sciences, Texas A&M University – Corpus Christ.

Yonge, C.M. (1960). *Oysters*. Collins, London. 209 pp.