Essential Fish Habitat Source Document:

Red Deepsea Crab, Chaceon (Geryon) quinquedens,
Life History and Habitat Characteristics

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Red Deepsea Crab, *Chaceon (Geryon) quinquedens*,
Life History and Habitat Characteristics

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Species Names: The NMFS Northeast Region’s policy on the use of species names in all technical communications is generally to follow the American Fisheries Society’s lists of scientific and common names for fishes (i.e., Robins et al. 1991), mollusks (i.e., Turgeon et al. 1998), and decapod crustaceans (i.e., Williams et al. 1989), and to follow the Society for Marine Mammalogy’s guidance on scientific and common names for marine mammals (i.e., Rice 1998). Exceptions to this policy occur when there are subsequent compelling revisions in the classifications of species, resulting in changes in the names of species (e.g., Manning and Holthius 1989, Cooper and Chapleau 1998, McEachran and Dunn 1998).

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Editorial Notes

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Statistical Terms: The NEFSC Editorial Office’s policy on the use of statistical terms in all technical communications is generally to follow the International Standards Organization’s handbook of statistical methods (i.e., ISO 1981g).

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FOREWORD

One of the greatest long-term threats to the viability of commercial and recreational fisheries is the continuing loss of marine, estuarine, and other aquatic habitats.

Magnuson-Stevens Fishery Conservation and Management Act (October 11, 1996)

The long-term viability of living marine resources depends on protection of their habitat.

NMFS Strategic Plan for Fisheries Research (February 1998)

The Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA), which was reauthorized and amended by the Sustainable Fisheries Act (1996), requires the eight regional fishery management councils to describe and identify essential fish habitat (EFH) in their respective regions, to specify actions to conserve and enhance that EFH, and to minimize the adverse effects of fishing on EFH. Congress defined EFH as “those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity.” The MSFCMA requires NMFS to assist the regional fishery management councils in the implementation of EFH in their respective fishery management plans.

NMFS has taken a broad view of habitat as the area used by fish throughout their life cycle. Fish use habitat for spawning, feeding, nursery, migration, and shelter, but most habitats provide only a subset of these functions. Fish may change habitats with changes in life history stage, seasonal and geographic distributions, abundance, and interactions with other species. The type of habitat, as well as its attributes and functions, are important for sustaining the production of managed species.

The Northeast Fisheries Science Center compiled the available information on the distribution, abundance, and habitat requirements for each of the species managed by the New England and Mid-Atlantic Fishery Management Councils. That information is presented in this series of 31 EFH species reports (plus one consolidated methods report). The EFH species reports comprise a survey of the important literature as well as original analyses of fishery-independent data sets from NMFS and several coastal states. The species reports are also the source for the current EFH designations by the New England and Mid-Atlantic Fishery Management Councils, and have understandably begun to be referred to as the “EFH source documents.”

NMFS provided guidance to the regional fishery management councils for identifying and describing EFH of their managed species. Consistent with this guidance, the species reports present information on current and historic stock sizes, geographic range, and the period and location of major life history stages. The habitats of managed species are described by the physical, chemical, and biological components of the ecosystem where the species occur. Information on the habitat requirements is provided for each life history stage, and it includes, where available, habitat and environmental variables that control or limit distribution, abundance, growth, reproduction, mortality, and productivity.

Identifying and describing EFH are the first steps in the process of protecting, conserving, and enhancing essential habitats of the managed species. Ultimately, NMFS, the regional fishery management councils, fishing participants, Federal and state agencies, and other organizations will have to cooperate to achieve the habitat goals established by the MSFCMA.

A historical note: the EFH species reports effectively recommence a series of reports published by the NMFS Sandy Hook (New Jersey) Laboratory (now formally known as the James J. Howard Marine Sciences Laboratory) from 1977 to 1982. These reports, which were formally labeled as Sandy Hook Laboratory Technical Series Reports, but informally known as “Sandy Hook Bluebooks,” summarized biological and fisheries data for 18 economically important species. The fact that the bluebooks continue to be used two decades after their publication persuaded us to make their successors – the 31 EFH source documents – available to the public through publication in the NOAA Technical Memorandum NMFS-NE series.

JAMES J. HOWARD MARINE SCIENCES LABORATORY
HIGHLANDS, NEW JERSEY
SEPTEMBER 1999

JEFFREY N. CROSS, CHIEF
ECOSYSTEMS PROCESSES DIVISION
NORTHEAST FISHERIES SCIENCE CENTER
INTRODUCTION

Deep-sea red crabs, *Chaceon (Geryon) quinquedens* Smith 1879 (Figure 1), are contagiously distributed along the continental shelf edge and slope of the western Atlantic, occurring mostly between 200 and 1800 m from Emerald Bank, Nova Scotia (and into the Gulf of Maine) and along the continental slope of the east coast of the U.S., into the Gulf of Mexico (Pequegnat 1970; Williams and Wigley 1977; Elner et al. 1987). Previous reports of the occurrence of *Geryon (Chaceon) quinquedens* off West Africa and elsewhere outside of the western North Atlantic continental shelf edge and slope (including Bermuda, Brazil, and Argentina) were found to involve several new geryonid species or mis-identifications (Manning and Holthuis 1981, 1986, 1989). The species’ distribution in the depths of the Caribbean Sea, around the West Indies Islands, and off northeastern South America remains uncertain (R. Manning, National Museum of Natural History, Smithsonian Institution, Washington DC, personal communication, January 2000).

The red crab, like most deep-sea organisms, is slow growing but reaches a maximum size of about 180 mm carapace width (CW) and may live for 15 years or more, although precise information on life span is lacking (Serchuk and Wigley 1982). While catches of red crabs have been noted since the early days of deep-sea trawling in the 1880s (McRae 1961), only since the late 1960s and early 1970s has there been an interest in developing a commercial fishery for this deep-water crab (Wigley et al. 1975). The interest since the 1970s in deep-sea red crab as a harvestable species is thought to be the result of a decline in other coastal and offshore crab and lobster fisheries (Gerrior 1981; Hastie 1995). A deep-sea red crab fishery (and for its sibling species, the golden crab, *Chaceon fenneri*) also developed slightly later in southeastern U.S. and Gulf of Mexico waters (Lindberg and Wenner 1990). To support the development of the red crab fishery, there have been a number of biological and technological studies that were summarized by Hastie (1995). Compared to some other commercially harvested deep-sea crabs, red crabs are medium sized. However, it is primarily the crabs’ relatively long (to 60 cm each) walking legs and attached body sections that reach the human consumer (Wigley et al. 1975). Larger (> 114 mm CW) male crabs have traditionally been the target of the fishery (Serchuk and Wigley 1982). They are harvested by trap and trawl, although most of the fishery is part-time or a by-catch from the offshore lobster or groundfish fishery and few fishermen pursue the fishery full time. As a result of this variable effort, annual landings have varied by an order of magnitude and also because the fishery is partially bycatch.

It is important to note that in the information sources reviewed here the size of the deep-sea red crab is usually reported as carapace width (CW); however, this dimension was not measured consistently, and sometimes included the posterior lateral spines [as on Northeast Fisheries Science Center (NEFSC) surveys], or sometimes the space between the notches forward of this spine, or at time the carapace width limits were unspecified. The percent contributions of the spines to carapace width, compared to inter-notch carapace width, for all size ranges are unknown, at present. Sometimes carapace length is presented, which is the distance between the rostral spine to posterior edge of carapace; this dimension is about 80-82% of the carapace width (Gerrior 1981).

LIFE HISTORY

A graphic summary of the life cycle of deep-sea red crabs was developed by Hastie (1995), based on the work of several researchers (Figure 2). In summary, the red crab’s life cycle is typical of most brachyuran crabs with male-female coupling when the mature female molts; fertilized eggs are brooded attached to the undersides of the females; larvae are released into the water column for distribution; and after several typical crab larval stages, juveniles settle to the seabed for a benthic existence through the rest of its relatively long life.

EGGS

Mature eggs are large and yolky for crustaceans and range in diameter from 484 to 846 μm, and are thought to be the largest eggs known for crabs with planktonic development (Haefner 1977, 1978; Hines 1982, 1988). As for most decapod crustaceans, red crab eggs are ovipositioned and held *en mass* on the female pleopods under their abdominal flap for up to nine months until the eggs hatch and the larvae are released into the water column (Haefner 1978). The development of the ova was described by Haefner (1978).

LARVAE

Larval biology for deep-sea red crab is poorly known as few zoea and megalops have been collected or identified in zooplankton collections. None were identified among the 4400 brachyuran crab larvae found in the 1977-1998 NEFSC MARMAP zooplankton collections (J. Goulet, NMFS, NEFSC, Narragansett Laboratory, Narragansett, RI, personal communication, December 1999). However, Roff et al. (1986) reported sparse collections (averaging < 10 per 500 m³ neuston tow) of the zoal stage (but not megalops) from off central Nova Scotia into the outer Gulf of Maine and over the northeast peak of Georges Bank. No other larval survey data is known for this species in the northwest Atlantic.
Much of what we know about the development of this stage comes from eggs that were collected from captured females and then hatched and raised in laboratories. Larval development was observed to consist of four zoal stages and a final megalopa. The zoa is typical in appearance to most brachyurans; i.e., with a large dorsal spine, and the megalops is also of a typical crab form (Perkins 1973). The larval stages of this species are relatively large in size compared to other brachyuran crabs (Sulkin and Van Heukelem 1980). Kelly et al. (1982) estimated that, depending upon the water temperatures and food encountered during development, the red crab larvae require about 23-125 days from hatching until the megalops settles. Larvae have been collected in surface waters in June, according to Serchuk and Wigley (1982), but details of these collections were unreported. Roff et al. (1986) also reported collections of these larvae in surface waters (< 40 m) near Nova Scotia.

**JUVENILES**

Settling is reported at a relatively large first post-megalop instar stage, about 4 mm CW (Van Heukelem et al. 1983). This large size at settlement may be an adaptation to slow post-settlement growth, in that a large size at settlement will reduce the time and number of instars required to reach maturity (Hines 1986, 1990). Growth of juveniles is also partially temperature dependent, as Van Heukelem et al. (1983) reported that juvenile crabs maintained at 9-15°C grew six time faster than those maintained at 6°C, and at least five molts are required to grow to about 20 mm CW.

**ADULTS**

Haefner (1978) and Van Heukelem et al. (1983) suggest that the red crab requires about 18-20 molts before it reaches its maximum size of about 180 mm CW. Based on tagging studies, older crabs might molt infrequently, and intermolt periods can be 6-7 yrs for larger crabs, > 100 mm CW (Gerrior 1981; Lux et al. 1982). Molting can increase carapace size by about 7-12% and body weight by about 33% (Serchuk and Wigley 1982). The degree of chitinoclasia (black shell disease) and barnacle colonization on red crab carapaces (see the Natural Mortality and Competition sections below) was suggested as useful indicators of the length of time since a red crab's last molt (Haefner 1978).

Van Heukelem et al. (1983) believed that red crabs begin to recruit to the fishery at about 114 mm (CW), which corresponds to an age of about 5-6 yrs. Van Heukelem et al. (1983) also reported that male red crabs reach a maximum size of about 150 mm CW and females are slightly smaller, about 140 mm CW. Gerrior (1981), however, reports larger maximum sizes for males, 178 mm CW, but a smaller maximum size, ~ 120 mm CW, for females.

Farlow (1980) developed the following size-weight regressions for red crabs:

\[
\text{Males: } \log_{10}W = 3.09970 \log_{10}D - 0.59763 \quad (r = 0.96717, \ p = 0.00001, \ N = 140); \\
\text{Females: } \log_{10}W = 2.75225 \log_{10}D - 0.34986 \quad (r = 0.87320, \ p = 0.00010, \ N = 110); \\
\text{All: } \log_{10}W = 3.26202 \log_{10}D - 0.80350 \quad (r = 0.97126, \ p = 0.00001, \ N = 263); \\
\]

where \( W \) = grams (wet weight) and \( D \) = cm (posterior lateral spine, point-to-point carapace width). It is noted that this width measurement (D) may be slightly larger than the carapace widths noted in other studies which did not include the lateral spines in their measurements; for example, Gray (1970) measured carapace width between the notches anterior to this spine. Farlow (1980) found the size-weight relationship was curvilinear for both sexes, with weight gain per growth in width slow at carapace widths below ~ 80 mm, but above 80 mm CW, weight increased rapidly with carapace width expansion. Haefner (1978) reported a similar relationship, as did Twigg et al. (1997) for the Gulf of Mexico population, and they also noted that the size and weight structure of red crabs in the Gulf of Mexico was similar to the population on the Atlantic slope.

**REPRODUCTION**

Haefner (1977) reports the size at maturity of red crabs off Virginia was between 80-91 mm CW. Several studies reported ovigerous crabs are found primarily at sizes between 80-130 mm CW (Wigley et al. 1975; Haefner 1977; Hines 1988), although some egg-bearing red crabs were observed as small as 61 mm CW (Elner et al. 1987). Lawton and Duggan (1998) suggest that males smaller than 115 mm CW may be functionally immature. Mating behavior is considered typical of other crabs (Hastie 1995). The amount of time a male encases a recently molted female can be several weeks (Elner et al. 1987). The opposite sexes probably rely on pheromones to find each other for mating (Hines 1990), and pheromones are useful if each sex has different preferred depths of occurrence during non-mating periods. Egg mass can be as much as 22% of female body weight, which is much higher that the average 10% for almost all other crabs (Hines 1982). Female red crab fecundity has been estimated to range from 36 x 10³ to 226 x 10³ eggs per female, and is directly related to female body size (Hines 1988).

Erdman et al. (1991) suggested that the egg brooding period may be about nine months, at least for the Gulf of Mexico population, and larvae are hatched in the early
spring there. There is no evidence of any restricted seasonality in spawning activity in any geographic region of the population, although a mid-winter peak is suggested as larval releases are reported to extend from January to June (Wigley et al. 1975; Haefner 1978; Lux et al. 1982; Erdman et al. 1991; Biesiot and Perry 1995). Laboratory studies have also found hatching to occur from April to June (Perkins 1973). Gerrier (1981), however, suggested that red crab egg hatching occurred later, between July and October, based on the ratio of egg-bearing to non-egg-bearing crabs.

Because of the long intermolt period for adult females (5-7 yrs), and the assumption that like most other brachyurans fertilization only occurs at molting, it has been speculated that red crabs may not spawn annually, although it is possible that sperm could be stored for intermolt spawning efforts; thus there can be annual brooding within the population, although not for every mature individual (Hines 1982; Lux et al. 1982; Erdman et al. 1991; Biesiot and Perry 1995). Hines (1990) reports that there is no evidence of senility or any reproduction capacity decline at the largest sizes for the species. However, Lux et al. (1982) and Lawton and Duggan (1998) suggest that there is evidence for a terminal molt; this may restrict any significant increases in fecundity with age.

**FOOD HABITS**

No information is known on the natural diets of red crab larvae, but it is probably zooplanktivorous, as they were found to thrive on rotifers, brine shrimp, and chopped mollusk meats in laboratory cultures (Perkins 1973; Sulkin and Van Heukelem 1980; Van Heukelem et al. 1983). Sulkin and Van Heukelem (1980) believe that the ability of red crab larvae to develop with reduced growth on a relatively poor diet (i.e., rotifers) suggests an adaptation to patchy and often poor food resources in slope waters. This can also allow the larvae considerable flexibility in prey choice.

Farlow (1980) reported that red crabs are opportunistic feeders, a characteristic of many deep-sea organisms. He reported that post-larval, benthic red crabs ate a wide variety of infaunal and epifaunal benthic invertebrates that they find in the silty sediment or pick off the seabed surface (Gerrior 1981). This observation is supported by submersible observations of red crabs being commonly found in shallow pits and excavations in softer sediments, and by infaunal bivalve mollusks being found in red crab stomachs (Valentine et al. 1980). Farlow (1980) also reported that smaller red crabs ate sponges, hydroids, gastropod and scaphopod mollusks, small polychaetes and crustaceans, and possibly tunicates. Larger crabs ate similar small benthic fauna and larger prey, such as demersal and mid-water fish (Nezumia and myctophids were identified in red crab guts), squid, and the relatively large, epibenthic, quill worm (*Hyalinoecia artifex*). Farlow's (1980) finding of sponges, hydroids, and tunicates in the diets suggests that epifauna attached to solid surfaces are also preyed upon; such epifauna is most common within the deeper rocky areas of the Gulf of Maine and within submarine canyons. Gray (1970) reported that red crabs held in aquaria ate anemones by hovering over an anemone until it extended its tentacles, then it reached down with its chelipeds and gently pulled off and ate one tentacle at a time until the anemone was bare of tentacles. Farlow (1980) considered the red crab the dominant large predator of the biomass on the upper slope.

They can also scavenge deadfalls (e.g., trawl discards) of fish and squid, as they are readily caught in traps with these as bait (Gerrior 1981) and eat them when held in aquaria (Gray 1970). Olfaction appears to be important in locating foodfalls as they are reported to be attracted to bait within a several km radius (Diehl and Biesiot 1994). They also probably resort to sediment deposit feeding at times and consume anything else they might encounter that can provide sustenance, including man-made artifacts; e.g., wood chips, pieces of yellow rubber and glass tubing have been found in the stomachs of some red crabs (Farlow 1980). American lobsters are also known to eat such man-made artifacts in coastal waters (Steimle 1994).

Elner et al. (1987) reports that unlike other crabs, red crabs do not stop feeding during mating; this is possibly an adaptation to an uncertain food supply and an extended male-female coupling period. Farlow (1980) estimated that "average-sized" red crabs fed in laboratory aquaria ate an average of 0.32 g wet wt of prey per day.

**NATURAL MORTALITY**

There are few records of predation on red crabs and these are by several species of gadid fishes. Sedberry and Musick (1978) reported that the longfin hake (*Urophycis chuss*) ate red crab as a minor prey. A search of the 1973-1990 NEFSC food habits data base (Reid et al. 1999) and shark prey data base found only a few instances of red crab identified as being eaten by, for example, cod (*Gadus morhua*) and red hake (*Urophycis chuss*), and there was no evidence of predation by larger sharks (W. Pratt, NMFS, NEFSC, Narragansett Laboratory, Narragansett, RI, personal communication, December, 1999). This lack of predation is unexpected as they do not have any obviously strong defensive mechanisms (they are non-burrowing, relatively slow moving, and weakly spined) and, as prey, they have a food energy value that is mid-range for deep-sea benthic crustaceans (Steimle and Terranova 1988). Farlow (1980) reports fresh red crab shell remains in the stomachs of larger crabs, suggesting a possibility of cannibalism; he discounted the possibility that these remains were
remnants of molted shells. Gray (1970) noted that red crabs tend to autonomize any legs that are damaged; this can also be a source of any red crab fragments found in stomachs.

The pathology of deep-sea red crabs is also poorly known. Red crabs have been reported often with dark lesions, shell disease, or chitinoclasia on their carapace (Hines 1990; Young 1991). These lesions are thought to be caused by bacteria that are found attached or adhering to the crab’s carapace; several bacterial taxa have been isolated from the infected lesions (Bullis et al. 1988). An association of the lesions with a former deep-water sewage sludge disposal activity was tentatively implicated as a cause of these lesions, although there is insufficient evidence to fully support such an association because a relatively high incidence of shell disease was also identified on specimens collected and preserved during the late nineteenth century, well prior to any substantial offshore waste disposals (Young 1991; Hastie 1995).

Larger crabs are reported to have more incidences of lesions, probably because of a longer intermolt period, and the lesions are thought to disappear with molting (Young 1991). Diehl and Biesiot (1994) report that there is a notable relationship between the degree of multi locus heterozygosity (genetic variability) and shell disease in individuals of this species that is “novel”. The effect of the lesions on the health of red crabs is poorly known, although the lesions can affect marketability, if the crabs are sold whole. Red crabs do not appear to be susceptible to gaffkemia, or red tail disease, that occurs in the American lobster (Cornick and Stewart 1975).

The relatively long life span of red crabs potentially exposes them over an extended period of time to the accumulation of contaminants that become available offshore; e.g., from atmospheric deposition, currents, or waste disposal. Examinations of red crab tissues, however, have shown that levels of certain toxic metals are similar, but no higher, to that found for short-lived, coastal species (Greig et al. 1976).

**COMPETITION**

Although observations on competitive interactions of red crabs with other species are poorly known, Hines (1990) suggested that the strong-clawed Jonah crab, *Cancer borealis*, and the American lobster, *Homarus americanus*, may be competing with red crabs on the continental shelf edge, although the nature of this competition (food or habitat) has not been observed. Hagfish (*Myxine* spp.) and other scavengers can compete for deadfalls (Lockhart et al. 1990). A variety of benthivorous demersal fish that occur on the upper slope, such as those commonly found in red crab or deep-sea lobster traps, including cusk (*Brosme brosme*) (Stone and Bailey 1980), or observed by divers where red crabs occur, such as eelfish (*Aldrovandia affinis*), rattails (*Coryphanoïdes* sp.), white hake (*Urophycis tenuis*), and galatheid crabs (*Munida* sp.) (Whitlatch et al. 1990), can compete with red crabs for benthic prey. Near and south of Cape Hatteras, a larger geryonid crab – the North American golden crab, *Chaceon fenneri*, is also found on the upper slope and could be competing with *C. quinquedens* for some habitat space or other resources if the two species populations overlap in habitat use (Lockhart et al. 1990; Hastie 1995).

Although not strictly a competitive relationship, a number of macroscopic organisms are reported to live epizoically on the surfaces of the red crab shell; these commonly include some species of stalked or “goose” barnacles, which are filter-feeders. A commensal polychaete worm, *Dorveilla geryonica*, has been reported to inhabit the gill chamber of red crabs, but its source of food and effect on the crab is unknown (Gaston and Benner 1981).

**MIGRATION**

Tagging studies off southern New England by Ganz and Herrmann (175) and Lux et al. (1982) suggest adult red crabs move both up and down the continental slope, covering a range of about 500 m in depth, perhaps as part their spawning cycle. The adults were also found to move laterally almost 100 km along the slope, but most tag returns were from areas within 20 km of their release location. Movements of the tagged crabs within the ~200-1000 m depth zone, between Hudson and Block Canyons, seem to be generally without any predominant direction. Juvenile red crabs, which are thought to settle from their larval stage to the seabed in deeper mid-slope waters, are reported to move gradually upslope into shallower waters with growth (Wigley et al. 1975), but this may not be a true migration.

**STOCK STRUCTURE**

Wigley et al. (1975) reported a bimodal depth distribution in male and female red crab size frequency distributions south of Georges Bank, although Farlow (1980) and Gerrior (1981) found less distinct segregation of sexes in their studies. Lockhart et al. (1990) suggested that the habitat use and distribution of the Gulf of Mexico population of red crabs seems different from what has been reported for the Middle Atlantic Bight population. This suggests that there can be physiological tolerance differences between these two populations. However, Diehl and Biesiot (1994) reported that red crabs have a high degree of genetic variabilility, more so than other deep-sea crustaceans, which can mask evidence of a genetic separation trend.
HABITAT CHARACTERISTICS

The larvae of this species are pelagic and occur in warmer and lower salinity surface waters above and beyond the continental slope habitat frequented by adult females. Post-larval red crabs are primarily inhabitants of the silty seabed of the deep cold water on the outer continental shelf and mid to upper continental slope of the western North Atlantic, south of the Gulf of Saint Lawrence (Canada), into the partially rocky Gulf of Maine, and along the continental shelf edge and slope into the Gulf of Mexico, and possibly the western South Atlantic. These crabs are considered part of an assemblage of deep-water crustaceans that inhabit the mid to upper continental slope of the northwest Atlantic, and this assemblage includes a number of smaller shrimp and crabs (Wenner and Boesch 1979). Salinities on the upper slope where benthic red crabs occur tend to be stable and oceanic at about 35-36 ppt (Schmitz et al. 1987). The thermal regime can be more variable, ~ 4-10°C, and include the temporary warming effects of the passage of an inshore loop or gyre of the Gulf Stream along the upper slope and shelf edge.

EGGS

As for most decapod crustacea, the eggs of the red crab are attached en mass to pleopods under the abdominal flap of females until the eggs hatch and the larvae are released into the water column (Haefner 1978). Egg-bearing females are most commonly found on the shallow continental slope, between about 200-400 m, where temperatures are typically between 4-10°C (Wigley et al. 1975; Kelly et al. 1982; Lindberg et al. 1990). Gray (1970) suggested that egg-bearing females are common within submarine canyons off southern New England.

LARVAE

Sulkin et al. (1980) reported that early larval stages show positive phototaxis down to light intensities of 2 x 10^3 W/m². At lower intensities the majority of the larvae were indifferent or negatively phototactic. The larvae were also found to be able to swim through relatively sharp thermal gradients; e.g., 10°C. Kelly et al. (1982) believed that hatched zoa are negatively geotactic and positively phototactic; i.e., they tend to move upward in the water column, and somehow swim hundreds of meters to surface waters. During this ascent, they are thus exposed to changing thermal and prey and predator availability conditions. Roff et al. (1986) reported that the greatest collections of decapod crustacean larvae in Gulf of Maine and Nova Scotian waters, including that of the red crab, occurred in neuston samples from surface waters, < 40 m. Roff et al. also reported that the red crab larvae were collected in relatively low (averaging less than 10 per neuston tow) concentrations where surface salinities ranged between 28.9 and 33.0 ppt, and temperatures were between 6.0°C and 19.5°C. Kelly et al. (1982) reported that red crab larvae can survive temperatures as high as 25°C (as found at the summer sea surface and within parts of the Gulf Stream water mass).

Red crab larvae were also collected between 12 and 270 km offshore in the Nova Scotian-Georges Bank area and, based on a factorial analysis of crustacean larval abundance and distribution collection data, were not strongly associated with concentrations of any other larval crustaceans (Roff et al. 1986).

Red crab zoeal swimming activity slows down as they approach metamorphosis into the megalops or first crab instar stage, which serves to let the megalopa gravitationally (or actively?) descend to the seabed (Kelly et al. 1982).

JUVENILES

The benthic settlement of the first “crab” stage of red crabs is reported to occur in mid-slope water (~ 1000 m), but the growing juveniles may gradually move upslope to warmer, upper slope waters (Wigley et al. 1975). Wigley et al. (1975) reported that “young” red crabs were only collected in cold water, 4.4-5.5°C, which is characteristically found below the ~ 500 m lower limit of the shelf break “warm band” inhabited by tilefish, Lopholatilus chamaeleonticeps, and associated species (Steimle et al. 1999). This upslope movement can expose the juveniles to warmer water, and juvenile red crab growth rates were reported to increase as they are gradually exposed to warmer waters in the laboratory (Van Heukelem et al. 1983); this can be a survival enhancement adaptation. Availability of benthic prey may also be a factor in the upslope movement (if it is real), because the mean biomass of benthic infauna increases from 1000 m to 100 m in the Middle Atlantic Bight and New England (Wigley and Theroux 1981; Theroux and Wigley 1998). The juveniles were collected or observed on smooth or dimpled surfaced, silt-clay sediments (Auster et al. 1991), but might occur on other sediment types, especially in the heterogeneous sediment types of the Gulf of Maine and submarine canyons. Gray (1970) reported that the results of his trawl surveys suggested that submarine canyons off southern New England held concentrations of small crabs of both sexes.

The NEFSC collections of juvenile red crab from the bottom trawl surveys that are accompanied by hydrographic data are too few to summarize and draw any conclusions relative to their depth and temperature preferences and thus are not presented.

ADULTS

Like juveniles, adult red crabs are reported associated with smooth or dimpled, unconsolidated and consolidated
silt-clay sediments (Haefner and Musick 1975; Wigley et al. 1975; Valentine et al. 1980; Lindberg et al. 1990), although Schroeder (1959) reported that there were good catches from both hard and soft bottom grounds. However, Herrmann (1974) reported that pot (trap) catches on hard bottoms were small compared to pot catches on softer sediments. Haefner and Musick (1974) reported that catches were lower within Norfolk Submarine Canyon (off Virginia) than on the slope adjacent to the canyon; their report is consistent with Gray (1970) who also noted this inter-canyon habitat preference for adults (especially males) off southern New England. However, Valentine et al. (1980) reported that red crabs were common in Oceano-grapher Canyon on the southern edge of Georges Bank. Auster et al. (1991) reported submersible observations showing that red crab seem to have a completely random distribution across the seabed, at a depth of about 700 m, without any apparent aggregation nodes.

The upper thermal limits for the benthic red crab have been reported to be about 10-12°C (Haefner 1978), which is also typical of the shelf edge “warm band” favored by tilefish (Steimle et al. 1999), but red crabs were reported to exhibit thermal stress at temperatures above 10°C (Gray 1970; Serchuk and Wigley 1982). The NEFSC spring and fall bottom trawl survey data for small and large (i.e., harvestable-sized) adult red crabs collected at depths less than 400 m shows that, in the shallow edge of their known depth distribution, both size groups were most commonly collected at bottom temperatures of about 11°C in during the February-March spring surveys (Figure 3) and at slightly cooler areas of about 7-9°C during the September-November fall surveys (Figure 4). Both size groups were mostly collected at depths greater than 300 m in both seasons. They were also collected in minor quantities at a greater range of temperatures (3-14°C) and at depths as shallow as 80 m.

The upper depth limits of red crab occurrence along the slope overlaps the deep-sea oxygen minimum zone, which occurs at about 200-400 m along the slope; this zone is where dissolved oxygen concentrations (DO) can be as low as 3 ml/l, while DO concentrations above or below this minimum zone are usually about 5-7 ml/l (Flagg 1987; Schmitz 1987). The ability of red crab to tolerate hypoxic conditions reported by Henry et al. (1990a) and Erdman et al. (1991) seems an adaptation for adults to transcend or inhabit the upper slope oxygen minimum depth zone. Laboratory studies have found that red crabs are intolerant of salinities below 20 ppt (Henry et al. 1990b); however, these low salinity levels are unlikely to occur in the depths of the edge of the continental shelf.

Hastie (1995) believes that several submersible studies (e.g., Valentine et al. 1980; Whitlatch et al. 1990) suggest that red crabs can be locally important bioturbators of surface sediments (and associated infaunal communities) by their sediment digging and benthic foraging activities. This bioturbation was speculated to play an important role in maintaining deep-sea biodiversity.

Although red crabs are most often found in outer continental shelf and slope depths > 100 m, they are also reported at depths as shallow as 40 m in the Gulf of Maine (Lux et al. 1982). Red crabs have not been reported to be a common member of the tilefish pueblo village, burrow, or canyon community, although red crab and tilefish depth distribution zones overlap (Grimes et al. 1987; Cooper et al. 1987). Red crabs, however, can be common in some canyon systems, such as Oceano-grapher Canyon and others along southern New England (Gray 1970; Valentine et al. 1980).

Haeedrich et al. (1980) found red crab the second most abundant megafaunal species in the 653-1290 m depth zone off southern New England, after the northern cutthroat eel, Synaphobranchus kaupi. Hecker (1990) also included three other fish species as representative members of the megafaunal assemblage on the mid- to upper slope off southern New England: a grenadier (Nezumia spp.), the longfin hake (Phycis chesteri), and the witch flounder (Glytocephalus cynoglossus). To this assemblage that includes red crab, Farlow (1980) added offshore hake (Merluccius albidos) and the wolf eelpout (Lycenchelys verrilli).

Sexual separation in habitat use has been reported, with females being more abundant in shallower and warmer slope waters (Schroeder 1959; Haefner and Musick 1974; Wigley et al. 1975; Haefner 1978; Stone and Bailey 1980; Lux et al. 1982; Lindberg et al. 1990). Although the portion of the NEFSC bottom trawl survey results for red crab that includes sexual differentiation and temperature data is small (181 samples between 1963-1999), it suggests that within the relatively shallow, <400 m survey depth range, females were more commonly collected on about a 2:1 ratio than males, and females were slightly more common in the fall than in the spring. Because of the limited depth scope and sample size of the survey results, these tentative conclusions can be biased.

Known large scale disturbances on the continental slope can affect the red crab population, as well as most other benthic species that live there. One such disturbance is that in the past areas of the continental slope with soft sediments have become dislodged and slumped into deeper waters (Tucholke 1987). This can undoubtedly have an effect on biological populations in and near the slump zone. Another such disturbance was that which caused the mass mortalities of tilefish and associated organisms in 1880 (Steimle et al. 1999). Although the actual cause of the massive tilefish mortality is not known, the oceanographic or geological factors involved (assuming either of these was involved) in that event, which basically decimated the tilefish population and most other organisms associated with the warm band in the Middle Atlantic Bight for over a decade, could reoccur and also have an effect on the red crab population. A recent analysis suggests that anomalously cold water was in the area of the 1880s tilefish kill and...
probably responsible for the mortality event (Marsh et al. 1999).

GEOGRAPHICAL DISTRIBUTION

Post-larval red crabs are inhabitants of the seabed of the mid to upper continental slope of the western North Atlantic, Gulf of Mexico and possibly the northwestern South Atlantic, and the larvae inhabit the water column generally above and near the adult distributions. The NEFSC bottom trawl surveys collect small quantities of benthic red crabs, but these surveys are typically restricted to depths less than 400 m on the upper slope, although they occasionally trawl in deeper canyons (Reid et al. 1999). Fishery independent information of red crab distributions below this NEFSC bottom trawl survey depth limit are only available from infrequent, special surveys, such as those reported by McRae (1961), Haefner and Musick (1974), or Wigley et al. (1975).

EGGS

Egg-bearing females are generally found distributed on shallow slope waters of less than 400 m (Kelly et al. 1982) and from Nova Scotia to at least the Gulf of Mexico. As for most decapod crustaceae, eggs are held en mass on the pleopods under the female's abdominal flap until the eggs hatch and the larvae are released into the water column (Haefner 1978).

LARVAE

Larvae have been collected from off Nova Scotia (Roff et al. 1986), but have not yet reported from other areas where adults occur, including the Gulf of Mexico. In the northwest Atlantic, Kelly et al. (1982) suggested that because the early red crab larval stages seek surface waters and grow faster in warm water, the movement of the Gulf Stream [and its meanders and gyres] south of Georges Bank can have a role in larval dispersal. Larvae can tolerate water temperatures as high as 25°C, as would be found in Gulf Stream or South Atlantic Bight/Gulf of Mexico surface waters, as well as < 10°C, water temperatures found on the continental slope seabed. With offshore Nova Scotia being the northern boundary of where they are known to be found, if the Gulf Stream is a significant red crab larval dispersal factor, it is possible that a red crab larval source from as far south as the South Atlantic Bight can be important to juvenile recruitment in the New England area. However, there is general southerly shelf water movement inshore of the Gulf Stream affected area, and occasional southward moving Gulf Stream gyres or eddies can distribute the larvae from southern New England and Georges Bank spawning populations south to near Cape Hatteras, too (Kelly et al. 1982). Kelly et al. (1982) also estimated that the range of larval dispersal can vary with their position in the water column and season, and dispersal might range from about 150 to almost 1000 km from the hatching area. Kelly et al. (1982) also presented a larval dispersal model that suggested that recruitment to southern New England red crab stocks might be variable, while recruitment to the stocks off Virginia might be more predictable.

JUVENILES

Juvenile red crabs were reported or presumed to have the same latitudinal distribution as adults; i.e., occurring from Nova Scotia to at least the Gulf of Mexico. However, their distribution along the continental slope depth gradient within this range may differ from that of adults. Wigley et al. (1975) and Haefner (1977) believed that metamorphosing megalopa settle to the seabed at mid-slope depths (~1000 m) as first instar juveniles and move upslope gradually as they grow. This pattern of settlement and gradual redistribution was supported by an inverse relationship between body size and depth reported by Wigley et al. (1975). They also report that only small specimens are usually collected in deep water, 740-1051 m, off southern New England. On the Scotian shelf, however, a wider range of sizes were found at the 720-900 m depths (Stone and Bailey 1980), and no clear relationship between red crab individual weight and depth was found by Farlow (1980). McRae (1961) noted that most of the large numbers of red crabs collected in a 1955-1957 survey of the Gulf of Maine (i.e., generally at depths of less than 300 m) were "small"; but this shallow depth distribution of presumed juvenile red crabs could be also the result of an early 1950s strong year class using most acceptable habitats, or an unusual pattern of settling larvae.

In the ~ 400 m depth-limited 1964-1999 NEFSC bottom trawl surveys, juvenile red crabs (equal or less than 7 cm CW) were collected in small quantities (less than 6 per tow) mostly within the western Gulf of Maine and even less were collected on the continental shelf edge between southern Georges Bank and near Toms Canyon (Figure 5). Because of the depth limitations of the NEFSC surveys, their assessments of the distribution of red crabs are incomplete, and juveniles (and adults) that are known to occur deeper on the continental slope were not surveyed.

ADULTS

In the Northeast, adult red crabs occur along the continental shelf edge and upper slope from the Scotian Shelf and the Gulf of Maine to Cape Hatteras (Serchuk and Wigley 1982). The species also occurs south of Cape
Hatteras into at least the Gulf of Mexico at similar depths. For an examination of the 400 m depth-limited 1964-1999 NEFSC bottom trawl survey data, the adult red crabs were segregated into two groups for analysis: below harvestable-size (small) adults (8-11 cm CW; Figure 6) and large adults at or above the commonly used harvestable size of 11 cm CW (Figure 7). The small adults were not collected during the winter bottom trawl surveys and only a few were collected in the summer surveys within and around the perimeter of the Gulf of Maine, but during the spring and fall surveys, they were collected in minor to moderate numbers both within the western Gulf of Maine and along the outer continental shelf between southern Georges Bank and Norfolk Canyon (Figure 6). The larger, harvestable adults were collected in a similar pattern, although fewer of the larger crabs were collected within the Gulf of Maine during the spring and fall trawl surveys (Figure 7).

As previously noted, there may be an inverse relationship between body size and depth (Wigley et al. 1975). Stone and Bailey (1980) reported that large crabs were only collected at 180-360 m depths on the Scotian Shelf. In the Gulf of Mexico, red crabs were not commonly collected above the 677 m depth zone; temperature or bottom sediment type could be prime factors controlling their distribution in the Gulf of Mexico (Lindberg et al. 1990; Lockhart et al. 1990).

From around Cape Hatteras into the Gulf of Mexico, red crabs may partially overlap the distribution of a larger sibling species, the golden crab (C. feneri, previously called Geryon affinis), that was noted to occur uncommonly off southern New England, too (Wigley et al. 1975).

**STATUS OF THE STOCKS**

Although occasional surveys of the relative abundance and distribution of this species have been conducted since the 1950s in some areas (Schroeder 1959; McRae 1961; Haefner and Musik 1974; Wigley et al. 1975; Haefner 1978; Gerrior 1981; Stone and Bailey 1980; McElman and Elner 1982) there have not been any broad-scale, long-term, fishery-independent surveys for this species to document any trends in relative population abundance and distribution (F. Almeida, NMFS, NEFSC, Woods Hole Laboratory, Woods Hole, MA, personal communication, December 1999). Broad-scale pot surveys have not been done, either, although pots may be better collectors of red crabs than trawls (P. Gerrior, NMFS, NEFSC, Woods Hole Laboratory, Woods Hole, MA, personal communication, August 2000). Hastie (1995) summarized a number of previous stock assessments and density estimates for the species to the early 1990s, but these also included information from south of Cape Hatteras. Annual northeast landings were reported since the 1970s but the data were not comprehensive until the early 1980s (C. Yustin, NMFS, NERO, Gloucester, MA, personal communication, January 2000). Landings between 1982 and 1998 averaged overall about 1800 MT, but reported landings annually varied between a range of 0.25 and 3800 MT. Peak harvests were reported in 1984 and 1988, and an almost insignificant harvest was reported in 1994 (Figure 8); CPUE data are not available.

The slow growth and maturation rates of red crabs, and possible infrequent recruitment, suggests that the high yields of the 1970s-1980s will likely be unsustainable (Hastie 1995).

**RESEARCH NEEDS**

It is obvious more needs to be known about the distribution of the species at all life stages, the variability and trends in population abundance and dynamics, and a way to adequately sample larval stages. The studies on red crabs summarized above include some that present differing results or conclusions about the biology or habitat use of this species; e.g., do megalops settle in deeper water and move upslope with growth and are sexes distributed separately (Hines 1990)? These areas of conflicting information need to be resolved by further research or data analysis. Further research or data is also needed on: age-size relationships, lengths of intermolt periods for all size classes, mortality rates for various size classes (especially for discards), yield per recruit, upslope and lateral migrations (including for spawning or related to size class), Middle Atlantic Bight larval dispersal patterns and the testing of larval dispersal models, genetic comparison of the Northwest Atlantic and Florida/ Gulf of Mexico populations, and where and when females primarily spawn and the possibility of sperm storage by intermolt females (Kelly et al. 1982; Armstrong 1990; Lindberg and Wenner 1990; Lockhart et al. 1990; Hastie 1995). In the northeast the use of submarine canyons as preferred spawning and juvenile red crab nursery areas, as suggested by Gray (1970), needs to be re-examined and verified for the potential of this habitat being critical to the life history of the species. There is also a need to find a cost-effective approach to conducting stock assessment surveys of this and other harvestable deep-water species.

Beside these research needs, there is a need to standardize size measurements on red crabs, such as carapace widths, which should not include damageable or erodible rostral or lateral spines in the measurements, as was done in some studies. The carapace width between the notches forward of the outermost spine would provide a more consistent and reliable measure of size, and because the shell is relatively soft and can be bent with pressure, the measuring calipers should just touch the shell (Gray 1970).
ACKNOWLEDGMENTS

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REFERENCES CITED


Table 1. Summary of the life history and habitat characteristics of red crab, *Chaceon (Geryon) quinquedens*. (CW= carapace width.)

<table>
<thead>
<tr>
<th>Life Stage:</th>
<th>Eggs</th>
<th>Larvae</th>
<th>Juveniles</th>
<th>Adults</th>
<th>Spawning Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size and Growth</td>
<td>Fecundity: up to ~ 226,000 eggs/female.</td>
<td>4 instar stages, then megalops stage settles to seabed.</td>
<td>4-70 mm CW; molting period extends with size.</td>
<td>80-180 mm CW’ molts every 6-7 yrs; CW increases 7-12% per molt.</td>
<td>Egg-bearing from ~ 70 mm to 140 mm CW.</td>
</tr>
<tr>
<td>Habitat</td>
<td>Attached to female abdomen until hatching.</td>
<td>Water column, outer shelf and slope.</td>
<td>Seabed, 700-1800 m.</td>
<td>Seabed, 200-1300 m.</td>
<td>Seabed, upper slope.</td>
</tr>
<tr>
<td>Temperature</td>
<td>~ 4-12°C.</td>
<td>~ 4-25°C.</td>
<td>~ 4-10°C.</td>
<td>~ 5-14°C.</td>
<td>~ 4-12°C</td>
</tr>
<tr>
<td>Salinity</td>
<td>~ 35 ppt.</td>
<td>29-36 ppt.</td>
<td>~ 35 ppt.</td>
<td>~ 35 ppt.</td>
<td>~ 35 ppt.</td>
</tr>
<tr>
<td>Dissolved Oxygen</td>
<td>~ 3-8 ml/l.</td>
<td>~ 5-8 ml/l.</td>
<td>~ 3-7 ml/l.</td>
<td>~ 3-8 ml/l.</td>
<td>~ 3-8 ml/l.</td>
</tr>
<tr>
<td>Predators</td>
<td>Unreported.</td>
<td>Unreported.</td>
<td>Longfin hake, other gadids.</td>
<td>Same as for juveniles (?)</td>
<td>Unreported.</td>
</tr>
<tr>
<td>Notes</td>
<td>Attached to female abdomen until hatching.</td>
<td>Early stages rise to surface; later stages gradually settle to the seabed.</td>
<td>May move upslope with growth.</td>
<td>Movements are generally limited to &lt; 50 km.</td>
<td>Occurs when female molts, inter-molt sperm storage possible.</td>
</tr>
</tbody>
</table>
Figure 1. The red crab, *Chaceon (Geryon) quincedens* Smith 1879.
Figure 2. Summary of the life cycle of the red crab, *Chaceon (Geryon) quinquedens* [from Hastie (1995), used with permission].
Figure 3. Distributions of small and harvestable-sized (large) adult red crabs relative to bottom water temperature and depth based on spring NEFSC bottom trawl surveys (1968-1999; all years combined). White bars give the distribution of all the stations, and black bars represent, within each interval, the percentage of the total number of red crab caught.
Figure 4. Distributions of small and harvestable-sized (large) adult red crabs relative to bottom water temperature and depth based on fall NEFSC bottom trawl surveys (1963-1999; all years combined). White bars give the distribution of all the stations, and black bars represent, within each interval, the percentage of the total number of red crab caught.
Figure 5. Seasonal distribution and abundance of juvenile red crabs (≤ 7 cm CW) collected during NEFSC bottom trawl surveys (1963-1999, all years combined).
Figure 5. cont’d.

RED DEEPSEA CRAB – Juveniles (< 7 cm CW)
Spring (1968 – 1999)
NEFSC Bottom Trawl Surveys

Crabs caught/station (excluding null stations):
Mean: 2 Min: 1 Max: 4

Length (cm):
Mean: 6 Min: 4 Max: 7
RED DEEPSEA CRAB – Juveniles (< 7 cm CW)
Summer (1964 – 1995)
NEFSC Bottom Trawl Surveys

Crabs caught/station (excluding null stations):
Mean: 2 Min: 2 Max: 2

Length (cm):
Mean: 7 Min: 6 Max: 7

Figure 5. cont’d.
RED DEEPSEA CRAB – Juveniles (< 7 cm CW)
Fall (1963 – 1999)
NEFSC Bottom Trawl Surveys

Crabs caught/station (excluding null stations):
Mean: 2 Min: 1 Max: 4

Length (cm):
Mean: 6 Min: 1 Max: 7

Figure 5. cont’d.
Figure 6. Seasonal distribution and abundance of small adult red crabs (8-11 cm CW) collected during NEFSC bottom trawl surveys (1963-1999, all years combined; none were collected in winter).
RED DEEPSEA CRAB – Early Adults (8-11 cm CW)
Summer (1964 – 1995)
NEFSC Bottom Trawl Surveys

Crabs caught/station (excluding null stations):
Mean: 1 Min: 1 Max: 2

Length (cm):
Mean: 10 Min: 8 Max: 11

Figure 6. cont’d.
RED DEEPSEA CRAB – Early Adults (8-11 cm CW) Fall (1963 – 1999) NEFSC Bottom Trawl Surveys

Crabs caught/station (excluding null stations):
Mean: 5 Min: 1 Max: 47

Length (cm):
Mean: 10 Min: 8 Max: 11

Figure 6. cont’d.
Figure 7. Seasonal distribution and abundance of harvestable-sized red crabs (> 11 cm CW) collected during NEFSC bottom trawl surveys (1963-1999, all years combined; none were collected in winter).
RED DEEPSEA CRAB – Harvestable Adults (> 11 cm CW)

Summer (1964 – 1995)
NEFSC Bottom Trawl Surveys

Crabs caught/station (excluding null stations):
Mean: 1 Min: 1 Max: 2

Length (cm):
Mean: 12 Min: 12 Max: 14
RED DEEPSEA CRAB – Harvestable Adults (> 11 cm CW)

Fall (1963 – 1999) NEFSC Bottom Trawl Surveys

Crabs caught/station (excluding null stations):
Mean: 4 Min: 1 Max: 58

Length (cm):
Mean: 13 Min: 12 Max: 22
Figure 8. Commercial landings for red crab in the northeast.
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