Atlantic States Marine Fisheries Commission

ADDENDUM XXIII TO AMENDMENT 3 TO THE INTERSTATE FISHERY MANAGEMENT PLAN FOR AMERICAN LOBSTER

Habitat Considerations

ASMFC Vision Statement:
Sustainably Managing Atlantic Coastal Fisheries

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Executive Summary

Addendum XXIII focuses on habitat components that play a vital role in the reproduction, growth, and the sustainability of commercial and recreational fisheries by providing shelter, feeding, spawning and nursery grounds for lobsters to survive. While the Addendum does not implement any changes to the lobster management program, it is intended to advance our understanding of the habitat needs and requirements of American lobster and provides the most current information to inform management decisions.

This Addendum replaces Section 1.4 of Amendment 3 to the American Lobster Fishery Management Plan.

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1. Habitat Considerations

1.1. Introduction

The Atlantic State Marine Fisheries Commission's (Commission's) involvement in habitat issues has grown with the broadening of fisheries management responsibilities and the evolution of ecosystem-based fishery management. Since 1990, the Fishery Management Plans (FMP) for Commission-managed species have included more specific habitat information and recommendations.

The Atlantic Coastal Fisheries Cooperative Management Act (ACFCMA) sets the basis for the regulatory fisheries management program of the Commission, and requires that Commission FMPs include a habitat component. ACFCMA also recognizes habitat impairment as an issue contributing to fisheries declines. In response to this mandate, the Charter developed to guide the Interstate Fisheries Management Program of the Commission directs that "conservation programs and management measures shall be designed to protect fish habitats." The Commission recognizes that habitat protection and conservation are an important component to successful fisheries management.

The mission of the Atlantic States Marine Fisheries Commission's Habitat Program is:

> *To work through the Commission, in cooperation with appropriate agencies and organizations, to enhance and cooperatively manage vital fish habitat for conservation, restoration, and protection, and to support the cooperative management of Commission managed species.*

Although fisheries resources directly depend on habitat, state fisheries agencies generally do not maintain regulatory authority for habitat conservation. However, states can benefit by working on these common habitat problems in a coordinated fashion. One of the primary goals of the Habitat Committee, as identified in its *Habitat Committee Guidance Document (2013)*, is to "identify, enhance, and cooperatively manage vital fish habitat for conservation, restoration, and protection, and supporting the cooperative management of ASMFC and jointly-managed species." Successful conservation of fishery habitat for managed species will depend on the identification, protection, restoration, and promotion of important habitat areas. In order to achieve this goal, the Habitat Committee is responsible for developing and/or updating the habitat sections of Commission's FMPs that will serve as tools for state and federal agencies for protecting fish habitats.

This Addendum was initiated by the Habitat Committee in 2012 in order to update the habitat section of the current American Lobster FMP, which was approved in 1997. It is intended to provide supporting information on American lobster habitat needs and concerns and does not impact current regulatory measures.

1.2. Components of Habitat

Habitat components are those elements that play a vital role in the reproduction, growth and sustainability of commercial and recreational fisheries by providing shelter, feeding, spawning, and nursery grounds for lobsters to survive (www.habitat.noaa.gov/index.html). Habitat components include temperature, salinity, dissolved oxygen, pH, light and photoperiod, substrate, oceanographic conditions, and diet (also reviewed in Mercaldo-Allen and Kuropat 1994, ASMFC 1997, 2009). For each component, a description and summary of habitat requirements, tolerances, and potential effects on lobsters is described for their early-life stages (eggs and larvae), as well as for juveniles and adults. A summary of key biological threshold values is given at the end of this section.

1.2.1. Temperature

Temperature is the primary driving force influencing lobster metabolism, activity levels, spawning, development, growth, and possibly life span (Hawkins 1996, ASMFC 1997, 2009). Lobsters of all life-stages are reported to live in areas that range broadly in water temperature from -1ºC to over 25ºC (Aiken and Waddy 1986, ASMFC 1997, 2009). Changes in temperature also have striking effects resulting in at least a two-fold increase in activity (e.g., heart and respiration rates) with each 10°C rise in temperature (i.e., Q_{10} temperature coefficient). Temperature has direct effects on physiological processes such as gas exchange, acid-base regulation, cardiac performance, and protein synthesis among others that can negatively affect these animals under stressful thermal conditions (Whiteley et al. 1997, Table 1).

Degrees Celsius	**-1**	**4**	**10**	**12**	**15**	**20**	**25**
Degrees Fahrenheit	30	39	50	54	59	68	77

Table 1. Temperature range and key values (converted to degrees Fahrenheit) that are relevant to lobster physiology and are provided here as a reference.

<u>Eggs & Larvae</u>
Temperature is the key factor that determines the length of time the eggs are carried and when eggs will hatch (Templeman 1940, Perkins 1972, Aiken and Waddy 1980, Tlusty et al. 2008, Goldstein 2012). Egg hatching typically occurs when surface water temperatures are generally > 12°C (MacKenzie 1988), between June-September but the timing of this event is highly dependent on the region. Closely coupled metabolic rates increase with temperature thereby modulating yolk absorption, growth, and ultimately, the survival of eggs (Pandian 1970, Helluy and Beltz 1991). Although optimal temperatures for lobster egg growth are not fully known, seasonally fluctuating temperatures result in disparate growth patterns and subsequently, differing hatch times (Sibert et al. 2004, Goldstein 2012).

Crustacean egg exposure to either prolonged warm or cold temperatures can have a deleterious effect on the use of their yolk reserves (Garcia-Guerrero et al. 2003, Manush et al. 2006), and it has been suggested that prolonged (more so than average) cold temperatures (< 4°C) negatively affect egg development in *H. americanus* (Waddy and Aiken 1995). However, seasonally changing temperatures, including a refractory period of 'normally' cold (wintertime) seawater temperatures (< 5°C) are important to conserving egg resources for more rapid increases in temperature (> 10°C) that typically occur later in the season and precede hatch (Waddy and Aiken 1995). These kinds of seasonally- fluctuating thermal conditions were simulated in laboratory studies and resulted in egg development that extended well into the spring and early summer (see Table 2 in Perkins 1972, Gendron and Ouellett 2009, Goldstein 2012).

For both lobster eggs and early-stage larvae, lipids are considered a major energy reserve and are also used as structural components of cell membranes that are being formed as they grow

(Sasaki et al. 1986). Lipid depletion rates in lobster eggs are directly related to incubation temperatures. Yolk lipids tend to become catabolized first followed by yolk proteins. These ratios change and can be used to estimate the cost of egg development at differing temperatures (Sasaki et al. 1986). Over prolonged cold temperatures or those conditions in which temperatures are too high for even short periods of time, some crustacean embryos may instead utilize proteins as an energy source if lipids are low due to thermally-induced demands (Conceicao et al. 1998). However, Sasaki et al. (1986) showed that up until Stage IV (post-larval), lobsters depended upon stored capacities of lipids and that these residual lipids may be favorable to settlement processes. Temperature also has a direct influence on the success of egg clutch attachment and even egg retention and loss. Talbot et al. (1984) discovered that elevated winter temperatures prior to spawning have an adverse effect on egg retention. Other laboratory studies implicate elevated temperatures in a significant loss of extruded eggs as well as their attachment to the abdomen, ultimately influencing hatching success (Talbot and Harper 1984). Observations from field data (undocumented to-date) have also seen such a pattern in some areas.

After hatching, young lobsters pass through one pre-larval and four free-swimming larval (zoeal) stages (distinguished by morphological, behavioral, and physiological attributes) before settling to the bottom and molting into juveniles (Hadley 1908, Lawton and Lavalli 1995). All larval stages are normally completed in 25-35 days (Herrick 1895, see Table 1 in Templeman 1940), but their pelagic duration is highly temperature dependent, and it has recently been suggested that it is markedly shorter than previously thought (Annis et al. 2007). MacKenzie (1988) demonstrated via a series of laboratory rearing studies that if larvae hatch at 10°C they can develop successfully through Stages I and II; however, beyond that, warmer water is needed to complete their development to Stage IV and the early benthic juvenile phase, Stage V (4% larval survivorship at 10°C vs. 56% at 12°C larval survivorship, MacKenzie 1988). Similarly, Sastry and Vargo (1977) reported significantly lower survivorship to stage V at 10°C. Harding et al. (1983) also showed that larval hatching usually occurred when water temperatures rose above 12.5°C. This waiting period may optimize development, growth, and survival of larvae. Changes in the thermal environment (e.g., seasonal fluctuations, rates of change) can have significant physiological influence over total time to egg development as well as timing for the postlarval stage to recruit to the fishery (Templeman 1940, Hofmann and Powell 1998, Goldstein 2012).

Juveniles & Adults

Differences in temperature also can influence juvenile growth patterns (e.g., onset of molting in juveniles or the start or spawning in adults) between regions (Little and Watson 2005). Variations among thermal regimes have been documented to influence lobster size at maturity and overall somatic growth (Estrella and McKiernan 1989, Little and Watson 2005, Wahle and Fogarty 2006, Bergeron 2011). There is a strong influence of water temperature on most aspects of lobster reproduction including maturation, spawning, molt cycle, oogenesis and hatching (see Waddy and Aiken 1995 for review). While elevated temperatures accelerate the onset of reproductive maturity, low temperatures tend to delay ovarian maturation (Templeman 1936, Waddy and Aiken 1995).

Adult lobsters respond to small changes in temperature as demonstrated in previous work (e.g., Crossin et al. 1998, Jury and Watson 2000, Childress and Jury 2006), and they respond both behaviorally (e.g., movement) and physiologically (e.g., changes in cardiac cycle) (McLeese and Wilder 1958, Worden et al. 2006). Crossin et al. (1998) showed that lobsters tend to avoid water temperatures below 5°C and above 18°C and exhibit a thermal preference of 15.9°C; this is similar to the value of 16.5°C found by Reynolds and Casterlin (1979). Recent laboratory work on lobsters in Long Island Sound (LIS) has shown that as water temperature increased beyond a threshold of ~ 20.5°C, the respiration rate of lobsters increased significantly leading to stress (Powers et al. 2004, Dove et al. 2005). Lobsters tend not to be directly stressed by water temperatures below 20ºC as long as oxygen levels are maintained at > 2 mg O_2L^{-1}. Lobsters held at 21ºC and 23ºC had significantly higher respiration rates than those held at 18ºC and 19.5ºC (Powers et al. 2004). McLeese (1956) gave us insight into the survivorship of lobsters subjected to combinations of varying temperatures, dissolved oxygen, and salinity (see Figure 11 in Fogarty et al. 2008), since biological oxygen demand increases as temperatures increase; likewise, oxygen solubility in seawater diminishes. A key point is that lobsters exposed to seawater temperatures below 20ºC are not generally stressed as long as oxygen concentrations remain > 2 mg O_2L^{-1} and, recent work with lobsters in LIS, confirmed that water temperatures > ~ 20.5ºC induced respiratory stress (Powers et al. 2004, Dove et al. 2005). Thus, 20.5ºC appears to be a key physiological threshold value for lobsters in LIS and possibly other areas.

Worden et al. (2006) demonstrated that cardiac performance (heart rate) is strongly modulated by temperature and cardiac output is maximal at 10ºC and decreases significantly > 20ºC. In-tandem with this finding, Camacho et al. (2006) determined that the upper thermal limit for heart function is more than 20°C warmer than body temperature for lobsters acclimated to cold (4°C) temperatures whereas warm (20°C) acclimated lobsters are living within 10°C of their thermal trigger for heart failure at 30°C, suggesting that the threshold for heart failure is affected by acclimation temperature.

Finally, some studies suggest that although a great deal of lobster activity and locomotion is attributed to temperature, not all temperature ranges demonstrate this relationship (Jury et al. 2005, Langley and Watson 2011). McLeese and Wilder (1958) found a positive relationship at temperatures < 10°C, while others found a negative correlation at excessively warmer temperatures, > 20°C (Courchene and Stokesbury 2011).

1.2.2. Salinity

Salinity tolerance varies with developmental stage. Charmantier et al. (2001) provides an excellent review of the ecophysiological adaptation by lobsters to salinity throughout the life cycle. In general, the capacity to osmoregulate varies with development when exposed to low salinity. Furthermore, because lobsters can be found inhabiting shallow coastal areas, bays, estuaries and subtidal areas, they are frequently subjected to dramatic fluctuations in salinity (e.g., abnormal spring run-off and large storm events, Jury et al. 1995) where they may be subjected to short-term exposure to wide ranges in salinity.

<u>Eggs & Larvae</u>

The complex morphology of lobster eggs makes them particularly impenetrable to outside fluids (Talbot and Goudeau 1988, Johnson et al. 2011). However, the permeability of lobster eggs increases close to hatch, resulting in an osmotic uptake of water and the rupture of the membrane (Pandian 1970). For the most part, egg membranes act to osmotically buffer the variations of external salinities. Late-stage eggs carried by ovigerous females died within two hours of exposure to 17 ppt but could tolerate 24 ppt for at least 12 hours (Charmantier and Aiken 1987). Larvae seem to be less tolerant of changes in salinity but were found to progress through all Stages of development between 15-17ºC at 17 ppt (Templeman 1936), while Sastry and Vargo (1977) noticed that larval development to Stage V (early juvenile phase) slowed in salinities above 20 ppt at 15°C and 15 ppt at 20°C. Also, at 20°C, 48 h mortality (LD_{50}) ranged from14-18 ppt in larvae, was maximal at metamorphosis and decreased to approximately 12 ppt in postlarvae; 48 h LD_{50} was ~10 ppt in 1-year-old juveniles (see Table 1 in Charmantier et al. 2001). Therefore 1-year old lobsters appear to tolerate lower salinities better than young-of-year (YOY) animals.

Juveniles & Adults

The energetic demands on juvenile and adult lobsters engaged in osmoregulation influence their distributions and movements, particularly in estuarine habitats (Watson et al. 1999) and their ability to osmoregulate is heavily influenced by temperature (Charmantier et al. 2001). As a result, adult lobsters adopt behavioral strategies to avoid low salinity (Jury et al. 1994a,b, Childress and Jury 2006). For example, adults vacate their shelters at salinities < 12 ppt. Adults prefer higher salinities (20-25 ppt) over lower ones (10-15 ppt) (Jury 1994a). Females appear much more sensitive to reduced salinity and thus males appear to populate certain estuarine waters and bays on a seasonal basis (Jury et al. 1994a,b, Jury and Watson 2012). A detailed examination of the seasonal movements of lobsters into a New Hampshire estuary (Great Bay), showed that movements occurred in the spring when salinities were > 15 ppt (Watson et al. 1999).

1.2.3. Dissolved Oxygen

Eggs & Larvae

Studies in brachyuran crabs (*Cancer spp.*) provide direct evidence between active brood care and oxygen provision. For example, it has been shown that oxygen may be a critical factor in some brooding behaviors (egg-fanning, movement) (Baeza and Fernandez 2002, Romero et al. 2010). Because *H. americanus* also exhibits prolonged maternal care of its brood (e.g., ventilation and fanning of eggs), it is probable, but not documented, that ovigerous females require different conditions to successfully maintain egg clutches through to hatch and may select habitats that contain sediments providing a high rate of oxygen exchange (e.g., Dungeness crabs, Stone and O'Clair 2002). For larvae, dissolved oxygen (DO) concentrations < 1.0 mg O_2L^{-1} and pH levels < 5.0 and > 9.0 are lethal (Ennis 1995). Miller et al. (1992) found that larval-stage lobsters appear twice as sensitive as juveniles and adults to reduced DO. However, since larvae are planktonic, spending a good deal of time in the upper portion of the water column, they are apt to encounter continuously sufficient levels of DO.

Juveniles & Adults

Lobsters require more oxygen as water temperature increases and hypoxic waters become more stressful as they warm. The lower lethal oxygen level for juveniles and adults ranged from 0.2 mg O_2L^{-1} at 5°C to 1.2 mg O_2L^{-1} at 25°C in 30 ppt (Harding 1992). A study conducted in Western Long Island Sound (WLIS) showed that in general, the threshold of adult lobsters to critical DO levels is high compared to other marine species (finfish and squid), and these lobsters demonstrated a behavioral avoidance of DO levels < ~2.0 mgL^{-1} (Howell and Simpson 1994). Prior to molting, juveniles and adults become more susceptible and sensitive to low DO as oxygen consumption peaks at molting (Penkoff and Thurberg1982) and molting lobsters have been found to be less resistant to high temperature and low DO and salinity than lobsters during intermolt periods (Waddy et al. 1995).

Other reports document congregations of lobsters in large numbers near the edges of hypoxic zones where DO was > 2 mgL^{-1}. These lobsters moved away from other areas where DO dropped below 2 mgL^{-1}, thereby concentrating some populations of lobsters in WLIS during a severe hypoxic event in 1999 (see review in Pearce and Balcom 2005). In a series of laboratory-based experiments, Robohm et al. (2005) demonstrated that lobsters exposed to a combination of organics (ammonia, sulfides), normal summer-time temperatures, and low DO became increasingly susceptible to disease (e.g., *Aerococcus viridans*). Similarly, at high water temperatures (24°C) lethal effects on disease-free eastern LIS lobsters were minimal as long as DO was kept high; low DO at 24°C killed 90% of the lobsters in eight days (Draxler et al. 2005).

1.2.4. pH

Larvae

Low pH or ocean acidification (OA) resulting from the global increase in atmospheric CO_2 concentration may become an emerging threat to lobsters as has already been documented in the congener *H. gammarus* where Arnold et al. (2009) showed that larvae cultured in acidic seawater exhibited compromised exoskeletons (disruption of the calcification process) and decreased carapace masses. For *H. americanus* Hall and Bowden (2012) investigated the difference in development of newly hatched larvae until 90 days post-hatch when exposed to levels of low pH using morphological analysis, carapace calcification, and molecular expression of immune parameters. Preliminary results indicate that chronic exposure to low pH can have a detrimental impact on larval development. Based on ocean pH levels predicted for 2100, Keppel et al. (2012) studied the effects of reduced seawater pH on the growth (carapace length) and development (time to molt) of *H. americanus* larvae through Stages I-IV and determined that larvae in acidified seawater (pH = 7.7) exhibited a significantly shorter carapace length than those in control (pH = 8.1) seawater at each stage and also took significantly more time to reach each molt than control larvae. Thus, for the few studies we do have data for the effects of OA appear to slow overall development and stunt growth.

Juveniles & Adults

Few studies of OA and its effects on juvenile or adult lobsters have been reported. In European lobster (*Homarus gammarus*) Agnalt et al. (2013) noted deformities in both larvae and juveniles exposed to lower pH at two different temperatures. In *Homarus americanus* juveniles showed increased their calcification by 600% under high CO_2 levels (CO_2 = 2800 μatm) for 60 days but with high mortality rates (Ries et al. 2009). The combination of warmer temperatures and predicted levels of OA, would likely contribute to additional metabolic stress on juvenile lobsters, as seen in the crab *Hyas araneus* (Walther et al. 2010). In longer-term studies the effects of exposure to forecasted levels of OA were examined by Long et al. (2013) on the growth, condition, calcification, and survival of juvenile red king crabs, *Paralithodes camtschaticus*, and Tanner crabs, *Chionoecetes bairdi*. One dramatic result was that 100% mortality of red king crabs was reported after 95 days at a seawater pH of 7.5. Similarly to larval lobsters, there was a noticeable a decrease in survival for both species and may have serious negative impacts in lobsters as well.

1.2.5. Light & Photoperiod

Eggs & Larvae

There is evidence to suggest early larval stages are positively phototactic and later stages are capable of vertical migration in the water column (Fogarty 1983). Templeman and Tibbo (1945) noted that Stage III and IV larvae are less sensitive to light levels than early stages. A minimum light intensity is required to attract larvae to the sea surface but early-stage larvae seek lower depths in bright sunlight (Templeman 1933). Larval survival was found to be higher in low-light environments and larvae cultured in continuous darkness developed faster and were almost twice the weight of larvae grown in a photoperiod of 12:12 light:dark (LD) (Eagles et al. 1986).

Juveniles & Adults

Previous studies have demonstrated that daily rhythms in lobsters are influenced by endogenous circadian clocks, synchronized to natural LD cycles (Lawton and Lavalli 1995). A recent laboratory study by Langley and Watson (2011) found that lobsters are more nocturnal than diurnal and that activity peaks before dawn and after dusk. In addition, the reported presence of a light-sensitive molecule, cryptochrome, in the ventral nerve cord of lobsters suggests that this compound may play a role in lobster orientation and movement (White et al. 2012). For pre-ovigerous adult females, at low temperatures reproduction seems to be regulated by temperature, but at elevated temperatures photoperiod becomes the more overriding factor, especially if winter water temperatures remain elevated (Hedgecock 1983, Aiken and Waddy 1980, 1990). In a field study of LIS lobsters, Weiss (1970) found that light intensity strongly affected burrow occupancy and foraging behavior. Juvenile lobsters usually stayed in their burrows whenever ambient light intensity exceeded 0.04 μWcm^{-2}. Lobsters first emerged from their burrows ~25 min. after sunset at an underwater light intensity of 0.02 μWcm^{-2} from June-November. From December-January, lobsters did not appear until 40 min. after sunset when light intensity was less than that level (Weiss 1970, Lavalli and Lawton 1995).

1.2.6. Substrate

Postlarvae

Pre- and postlarval (Stage IV) selection of substrate types are complex processes (Boudreau et al. 1990, Cobb and Wahle 1994, Wahle and Incze 1997). Postlarvae utilize a variety of habitat types (e.g., nearshore rocky areas, offshore canyons, enclosed embayments, estuaries) that differ in their abiotic and biotic features over spatial and temporal scales (Wahle 1993, Wilson 1999, Wahle et al. 2013). Although subtidal cobble beds are largely considered preferred settlement areas (Wahle and Steneck 1991), the plasticity in substrate settlement choice remains broad (Caddy 1986). Howard and Bennett (1979) and Pottle and Elner (1982) found that lobsters tend to choose gravel rather than silt/clay substrates. Cobb et al. (1983) and Able et al. (1988) both found that postlarvae settle rapidly into rock/gravel, macroalgal-covered rock, salt-marsh peat, eelgrass, and seaweed substrates. Barshaw et al. (1985) and Barshaw and Bryant-Rich (1988) observed that postlarval lobster settled quickly into eelgrass, followed by rocks with algae in sand, then mud. In addition, the presence of biologically relevant odor plumes (adult conspecifics and macroalgae) and the existence of a thermocline have been reported to impact postlarval substrate selection especially in shallow habitats (Boudreau et al. 1991, 1993). Wahle et al. (2013) recently documented settled lobsters as deep as 80 m, although most were abundant above the thermocline (typically < 20 m, Boudreau et al. 1992) in summer-stratified regions (e.g., W. Gulf of ME and S. New England); likewise, depth-related differences were diminished in thermally mixed waters. A settlement (time series) index for American lobster has been formally established for lobster nursery habitats in both the northeast US and Atlantic Canada and remains active (see Wahle 2009, Wahle et al. 2013).

Juveniles & Adults

As in larvae, juveniles are distinguished by their ecological ontogeny until functional maturity and adulthood (see Lawton and Lavalli 1995). Lobsters may not leave their burrows until they reach a carapace length (CL) between 20-40 mm (Barshaw and Bryant-Rich 1988). Lobsters in this early benthic phase (5-40 mm CL) were found by Wahle (1988) and Wahle and Steneck (1991) in midcoast Maine to be most abundant in cobble and macroalgal-covered bedrock and rare in featureless mud, sand, or bedrock. Short et al. (2001) found evidence of adolescent lobsters and their preference for eelgrass beds in the lower portion of Great Bay Estuary, NH and reported that in associated mesocosm experiments, lobsters (53-73 mm CL) showed a clear preference for eelgrass over bare mud.

It is difficult to conclude that shelter-providing substrate, cobble in particular, represents a natural demographic bottleneck when juvenile lobsters occur in other substrates (e.g., eelgrass, bedrock, and muds; Addison and Fogarty 1992). However, in the absence of shelter juvenile lobsters require substrate that they can manipulate to form a shelter, especially YOY lobsters (Lawton and Lavalli 1995). The range of habitat types available to juvenile lobsters increases as pressure from predation declines (Lawton and Lavalli 1995) and the need for specific shelter size may be resolved by the lobster's ability to manipulate its environment which can result in the construction of suitable shelter from otherwise uninhabitable substrate. The excavation of shelters under man-made objects is common among juvenile and adult lobsters and may be important on featureless bottom (Cooper and Uzmann 1977).

Finally, Geraldi et al. (2009) determined that lobster movements were influenced by the quality and type of substrates (e.g., rock vs. sand) through which they were moving. Based on tag returns, lobsters that were initially caught and released on sediment moved farther and faster than those initially caught in traps on rocky substrate. Even in some estuarine environments, complex hard-bottom areas between soft-sediment patches (e.g., eelgrass beds) can serve as corridors and passageways for decapod crustaceans engaged in short- or long-term movements (see Micheli and Peterson 1999).

1.2.7. Oceanography

Abiotic factors such as tidal fronts, internal wave slicks, turbulence, surface currents, wind and Ekman transport (among many others; reviewed in Shanks 1995) at the time (and site) of hatch set the initial conditions for larval dispersal, and vary depending on the timing of this event (Tlusty et al. 2008, Goldstein 2012). The residence time for lobster larvae in the water column is controlled predominantly by surface water temperatures and, to a lesser extent, by food availability (Phillips and Sastry 1980, Mackenzie 1988, Annis 2005, Annis et al. 2007). These two factors, temperature and food ultimately help to influence their final destination along with intrinsic larval behaviors (e.g., vertical migration and swimming, Harding et al. 1987, Ennis 1995).

In the Gulf of Maine (GoM) there is considerable variation in circulation patterns from year to year. Variations in temperature and volume of water flowing into the GoM (including freshwater input from rivers) along with atmospheric fluctuations (temperature and wind patterns) are all factors that significantly affect the scale and duration of GoM circulation features like water masses (different densities), gyres, and alongshore currents (Mountain and Manning 1994). Various sources and sinks have been suggested for lobster larvae (e.g., wind direction, nutrients, drift; Katz et al. 1994, Incze et al. 2006, Chassé and Miller 2010). Incze and Naime (2000) reported on cross-shelf transport and the ability of larvae to utilize onshore sea breeze transport towards shore. Recently, Xue et al. (2008) and Incze et al. (2010) identified sources and sinks for 15 coastal areas and modeled larval release and dispersal over a period of four months. The Southern New England (SNE) stock area is characterized by weaker tidal currents than the GoM and Georges Bank, and, as a consequence drift was found to be highly wind dependent, with tidal currents only influencing short term movements. Fogarty (1983) observed peak larval densities following periods of inshore winds in the days preceding sampling in Block Island Sound and identified offshore areas and LIS as larval sources. Lund and Stewart (1970) suggest that relatively high concentrations of larvae in western LIS are a result of surface currents creating a larval retention area.

1.2.8. Diet

Larvae

The natural diet of larval and postlarval lobsters includes the wide variety of phytoplankton and zooplankton available to them (Ennis 1995), but, for the most part is relatively unstudied as more diet studies have been conducted in relation to culturing larvae in hatchery-type settings (e.g., Conklin 1995). Unlike the earlier larval stages, Stage IV postlarvae show increased dependence on protein and sequester lipid stores (Ennis 1995).

Juveniles & Adults

Zooplankton has been shown to provide an adequate diet for the growth and survival of shelter restricted juveniles and supplements the diet of emergent phase juveniles (Barshaw 1989, Lavalli 1991). Despite these habitat differences, diet is fairly consistent for emergent and vagile phase juveniles and is dominated by mussels, lobsters, rock crabs (*Cancer spp.*) and gastropods (Weiss 1970). Plants may be actively selected, forming a functional nutritional component of the diet (Weiss 1970, Conklin 1995). Lobsters forage among a wide spectrum of plants and animals that include crustaceans, mollusks, echinoderms, polycheates, and macroalgae. Lobsters are also known to temporally shift their diet depending on season or habitat (Elner and Campbell 1987, Conklin 1995) and are considered keystone predators, capable of driving the trophic dynamics in many benthic communities (Mann and Breen 1972). There is typically peak feeding activity between June and July; feeding activity then remains high in September even as temperatures begin to fall; and females maintain a higher level of feeding activity than males, at least until mid-February (Lawton and Lavalli 1995).

Category	Life-Stage	Threshold Value	Reference
Temperature	Eggs	<5°C winter, 10-12°C hatching	1, 2
	Larvae	10-12°C	2
	Juveniles/Adults	5-18°C, preference ~ 16°C, 20.5°C stressed	3, 4, 5, 6
Salinity	Eggs/Larvae	< 17 ppt	7
	Juveniles/Adults	< 12 ppt	8
Dissolved Oxygen	Larvae	$< 1\ mgO_2L^{-1}$	9
	Juveniles/Adults	< 2 ppm	10
pH	Larvae	< 7.7 (Stages I – IV)	11
	Juveniles/Adults	n/a	

Table 2. A summary of key biological threshold values for *H. americanus*. References: (1) Waddy and Aiken 1995; (2) MacKenzie 1988; (3) Reynolds and Casterlin 1979; (4) Crossin et al. 1998; (5) Dove et al. 2005; (6) Powers et al. 2004; (7) Charmantier et al. 2001; (8) Jury et al. 1994; (9) Ennis 1995; (10) Howell and Simpson 1994; (11) Keppel et al. 2012.

Given the widespread use of baited traps in some areas, it is very likely that these components play a significant role in habitat in some areas. Since many lobsters enter and vacate traps repeatedly (Jury et al. 2001), it is likely that most lobsters feed from traps before they are finally captured. In areas of intense fishing pressure, trap bait may provide a significant energy subsidy, supplementing the natural food resources available on lobster grounds (Lawton and Lavalli 1995, Grabowski et al. 2010).

1.3. Anthropogenic & Ecological Impacts on Lobster Habitat Components

Coastal areas in general attract construction and land and water-based development activities, which in-turn contributes to cumulative impacts on coastal resources, including fisheries. These activities can introduce pollutants (through point and non-point sources), cause changes in water quality (temperature, salinity, dissolved oxygen, suspended solids), modify the physical characteristics of a habitat, or remove/replace the habitat altogether, all of which can result in adverse impacts (particularly near-shore) on American lobsters and their associated resources.

1.3.1. Dumping & Dredging

Human activities can have a significant impact on the lobster resource and its environment. Siltation and turbidity from deforestation, poor agricultural practices, urban development, quarrying, dredging, construction, or oil drilling can destroy lobster habitat and adversely affect larval growth, development, and survival (Aiken and Waddy 1986, Harding et al. 1982, Harding 1992).

Ocean dumping has been identified as another major problem for lobster especially when it results in burying gravel beds. "Ocean dumping of silt-clay over gravel may increase spatial competition among juvenile lobsters for shelter in remaining gravel habitat" (Pottle and Elner 1982). Ocean dumping can affect bathymetry, sediment grain size, and trace element concentration disturbing benthic biota and population structure (Aiken and Waddy 1986). The disposal of soft sediments from harbor dredging can directly impact lobster habitat and disrupt food resources; however, the dumping of coarse, uncontaminated material may enhance lobster habitat once it is colonized with prey organisms (Harding 1992). For over 60 years (1924-1986) a marine dump-site off New York in the New York Bight apex (12-mile site) received an annual average of 8 million metric tons of sewage sludge from sewer districts in the New York/New Jersey area (ASMFC 1997). This location, at the head of Hudson Canyon, has been noted for its heavy metal contamination, high fecal coliform counts, “black oozy substrate, and anoxic layer of bottom water”. The area has been largely devoid of fishing practices. An elevated incidence of shell disease in some animals (‘burn spot’, shell disease, or epizootic shell disease, undetermined) and black gill disease was observed in crustaceans collected at this site (Harding 1992).

Since dumping at the 12-mile site ended in 1987, followed by a shift to a deepwater, 106-mile site, studies have shown some improvement in contaminant levels, bacterial counts, and in the low dissolved oxygen readings, which previously characterized the area. However, shortly after dumping began in the 106-mile offshore site, reports by offshore fishermen indicated a high rate of shell disease (or related, see above) in both lobsters and rock crabs in that area and a concurrent decline in landings. As a result, a joint NOAA/EPA Working Group met between 1988 and 1989 to assess if a relationship existed between shell disease prevalence and crustacean population fluctuations, and to determine if shell disease is pollution-related and if it results in mortality (Sindermann 1996).

The working group concluded that, although mortalities from shell disease have been observed in laboratory or impounded situations, and shell disease may pre-dispose crustaceans to predation or disease-related mortality, there is no conclusive evidence that shell disease causes fluctuations in crustacean populations in the New York Bight apex (ASMFC 1997). Subsequent studies conducted in the 12-mile site have been unable to conclude if improvements in shell disease prevalence have occurred since the sludge dumping was suspended, due to highly variable data.

Dredging and drilling muds also can be toxic at lethal and sublethal concentrations. Pottle and Elner (1982) reported that dredging or smothering of 'nursery areas' occupied by juvenile lobsters could have serious consequences for future recruitment into commercial fishing areas. Potentially lethal components of drilling muds include petroleum hydrocarbons, asphalts, aromatic lignosulphates, heavy metals and calcium-like cations such as barium and strontium. Observed reactions of lobsters to these include, depending on the concentrations, impaired coordination, cessation of feeding, loss of mobility, and death. Inhibition of burrowing behavior of Stage IV and V lobsters has been demonstrated (Mercaldo-Allen and Kuropat 1994). Drilling muds also affect habitat by their tendency to settle in depressions or flow downhill, a particular problem for lobsters whose natural habitat is offshore canyon areas

1.3.2. Energy & Transportation Projects

The Federal Energy Policy Act of 2005 allows leases, easements, and rights-of-way for coastal and offshore project activities for "energy-related purposes or for other authorized marine-related purposes," and support for offshore operations and facilities (NMFS 2010). Therefore, there are likely many cases where these present and future activities could impact habitat for lobsters.

Federal offshore areas are also increasingly being used as sites for energy projects, such as wind farms and LNG (liquid-natural gas) terminals (e.g., Neptune and Excelerate offshore LNG facilities, see NMFS 2010) and related infrastructure, such as pipelines. These sites potentially compete with the commercial lobster industry for space and may impact the integrity of certain habitat types for lobster. The implementation of pipeline projects or their related facilities raises concerns about the impact that their placement could have on lobster mobility and lobster habitat. The HubLine natural gas pipeline (29.4 mi long and 24-30" diameter pipe) from Salem/Beverly to Weymouth was constructed by Algonquin Gas Transmission Company in Massachusetts Bay between 2002-2003, and prior to this, Massachusetts Division of Marine Fisheries (MADMF) undertook extensive assessments (commercial lobster sea-sampling, ventless lobster trap monitoring, and early benthic phase lobster suction sampling) to evaluate the impact of these pipeline activities (see Estrella 2009 for details). Results indicated that there was no definitive evidence found that surface-laid pipe or its trench construction blocked the seasonal inshore migration of lobsters.

Wind farm proposals are also becoming more popular and these proposed projects include the establishment of underwater platforms that could potentially influence lobster movement patterns and local current structure thereby influencing larval dispersal patterns, impacting predator-prey interactions, and altering dominant fishing practices. However, additional structures (e.g., submersed platforms) may potentially benefit lobsters with additional structured habitats. Cape Wind Associates (CWA) proposes to construct a wind farm on Horseshoe Shoal, located between Cape Cod and Nantucket Island in Nantucket Sound, Massachusetts (NMFS 2010). The CWA project would have 130 wind turbines located as close as 4.1 miles off Cape Cod in an area of ~24 mi^2 with the turbines being placed at a minimum of 1/3 of a mile apart. If constructed, theses turbines would preempt other bottom uses in an area similar to oil and natural gas leases. The potential impacts associated with the CWA offshore wind energy project include the construction, operation and removal of turbine platforms and transmission cables; thermal and vibration impacts; and changes to species assemblages within the area from the introduction of vertical structures (NMFS 2010).

1.3.3. Pollution & Water Quality

Lobsters are sensitive to chemicals and have been known to vacate areas that have been subjected to pollution. Connor (1972) estimated that larvae are more susceptible than adults. The effects of petroleum products, industrial chemicals, and heavy metals are well published and include reduced survival, molt inhibition, regeneration, malformation, and changes in metabolism, energetics, and behavior (Aiken and Waddy 1986). Other important human activities that may lead to pollution and lobster habitat destruction include landfills, dredging, dumping, industrial wastes, spills and sewage outfalls. Point sources of pollution come from industrial plants, such as pulp and paper mills, fish processing plants, textile mills, metal fabrication and finishing plants, municipal sewage treatment plants, and chemical and electronic factories.

Non-point sources are not as easily located. Rainwater runoff often contains pesticides from agricultural and forested areas along with hydrocarbons, heavy metals and organics from urban areas. It is not unusual for older cities to combine their storm drainage system with the sewer system that results in raw sewage discharges during times of overflow (Lincoln 1998). All of these pollution sources can have a tremendous impact on water quality and habitat preservation. These problems can be multiplied when the contaminants get into the sediments and then are disturbed by dredging. When contaminants are suspended in the water column they become available for uptake by many species (including lobsters) and can accumulate throughout the food chain.

Considerable research has been done on the effects of hydrocarbons and drilling fluids on lobsters (Atema et al. 1982). These studies show that "both the chemical toxicity in the water column and the physical effect of covering the substrate with drilling mud interfere with normal lobster behavior." For postlarval lobsters, sublethal effects included feeding and molting delays, severe delays in shelter construction, increased walking and swimming difficulties, and lethargy. Atema and others (1982) concluded "perhaps as little as 1 mm (~0.04 inches) covering of drilling mud may cause increased exposure to predators and currents, resulting in the substrate becoming unsuitable for lobster settling and survival."

Pesticides & Heavy Metals

Lobsters are highly sensitive to certain pollutants, particularly pesticides. Organochlorines (e.g., DDT, PCDD, endosulfan, endrin, dieldrin, chlordane), pyrethoid pesticides (e.g., permethrin, cypermethrin, and fenvalerate) and organophosphate pesticides have very low lethal thresholds for lobsters (Mercaldo-Allen and Kuropat 1994). The use of organophosphate pesticides (e.g., emamectin benzoate, azamethiphos) to treat sea lice infestations in aquaculture operations (typically salmonids) have negative impacts on lobsters as well. Abgrall et al. (2000) investigated the use of azamethiphos in relation to shelter use by juvenile lobsters in the laboratory. Results indicated that lobsters avoided high levels of azamethiphos by vacating their shelters and concluded that although concentrations used in the aquaculture industry (100 μgL^{-1}) are low and would not affect lobster shelter use, mortality would increase due to prolonged exposure time to this pesticide or, indirectly through the susceptibility of leaving a shelter. Waddy et al. (2007) reported that a similar pesticide (emamectin benzoate), added as a prescribed medicated treatment for ectoparasites in salmon feed was capable of disrupting molting in ovigerous lobsters (these animals molted prematurely and lost their eggs), but is not typically consumed at high enough doses (0.6-0.8 μg $EMBg^{-1}$ was considered high), to elicit such a response. However, the impacts of waste fish feeds and their attractiveness to lobsters in aquaculture operations is something that warrants further research.

Importantly, chemicals used in mosquito control may have volatile effects in some lobster populations. The pesticides malathion, resmethrin, sumithrin, and methoprene elicit negative sub-lethal effects on lobster immune systems and act as endocrine disruptors (from all life-stages). Many of these chemicals were routinely used throughout the New York Metropolitan area to control West Nile Virus and coincided with a mass lobster mortality event in WLIS in 1999 (CTDEP 2000). Subsequent laboratory studies (DeGuise et al. 2005, Zulkosky et al. 2005) have shown that both lobster larvae and adults are sensitive to these compounds however, the concentrations and degree to which these lobsters were exposed is not fully known though modeling research by Landeck-Miller et al. (2005) suggest that concentrations of pesticides in the near bottom waters of LIS during 1999 probably were not high enough to represent stress to lobsters.

Heavy metals such as arsenic, copper, mercury, cadmium, iron, zinc, and lead are toxic at various concentrations and the details of their toxicity throughout all lobster life-stages is given in Mercaldo-Allen and Kuropat Tables 2-29 (1994). Stage I lobster larvae are quite sensitive to heavy metals. Although mortality resulted from test exposures to all three metals, toxicity to mercury was the greatest for first stage larvae followed by copper, then cadmium. Exposure to higher concentrations of copper (56 vs. 30 mgL^{-1}) was necessary for a lethal effect on juveniles and adults. Only sublethal effects were observed in juveniles from significant cadmium contamination while adults were not affected (Mercaldo-Allen and Kuropat 1994). The exposure of lobsters to heavy metals in the laboratory produced sublethal effects including impaired chemoreception and biochemical changes.

Pollutants such as polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs), halogenated hydrocarbons, and detergents may not have detrimental effects upon lobsters themselves, but may render them unfit for human consumption. Large quantities of PCBs were discharged by electrical component manufacturers into New Bedford Harbor and the adjacent Acushnet River in Massachusetts over several decades (Weaver 1984). The harbor sediments and biota still contain relatively large concentrations of PCBs that resulted in a significant segment of this estuarine system being closed to commercial lobstering. PCBs and PAHs accumulate quickly in lobster tissues, especially in the hepatopancreas, and can be slow to depurate. Organic chemical exposure interfered with normal behavioral, chemosensory, and physiological processes. Industrial wastes resulted in significant lobster mortality by causing asphyxiation and/or cardiac function (Mercaldo-Allen and Kuropat 1994).

Oil Pollution

Many studies have been conducted on the effects of crude oil on lobsters. Toxicity varies with the level of refinement of oil and the concentration to which the animals are exposed

(Mercaldo-Allen and Kuropat 1994). For example, the more highly refined no. 2 fuel oil is more toxic than no. 6 oil. Responses to exposure range from mortality to sublethal effects of chemosensory interference or loss of coordination and equilibrium (Harding 1992). Larval forms are particularly sensitive since oil co-occurs in surface waters with them.

Oil pollution also severely and negatively affects the small food organisms critical to larval lobsters. Larvae which were fed oil contaminated *Artemia* spp. exhibited disruption in energetics (including reduced lipid levels), molting delays, reduced respiration rates, slowed growth rate, and changes in the oxygen/nitrogen ratio (Capuzzo and Lancaster 1981, 1982, Capuzzo et al. 1984, Mercaldo-Allen and Kuropat 1994). Oil pollution also affects lobsters in their adult stages. For example, laboratory studies have indicated that small quantities of crude oil can interfere with specific, perhaps chemosensory, behavior of lobsters. Feeding behavior has been shown in these studies to be affected, with the period between detection and attempted acquisition. Because of changes in feeding and other behaviors, it is possible that crude oil may interfere with the ability of male lobsters to detect sex pheromones released by female lobsters, which could severely interfere with reproductive activity.

Chlorine Toxicity

The effects and impacts of chlorine toxicity are related to the construction (some recent) and operation of chlorinated sewage outfall effluent. A MADMF report (2010) sought to assess if chlorinated sewage treatment plant effluent is having adverse effects on lobster abundance and the hard-bottom habitats utilized by lobster and other marine organisms in Massachusetts Bay and Buzzards Bay. Since 2000, sewage from the Greater Metropolitan Boston area is discharged into Massachusetts Bay through a 9.5-mile outfall pipe terminating in ~100-ft. deep waters. This effluent is discharged through more than 50 diffuser heads spanning the final ~1 mile of the outfall. Prior to 2000, sewage effluent for the Boston Harbor region was released through outfalls within the harbor. In one report (prior to the outfall's completion), Mitchell et al. (1998) concluded, “No impact is expected from residual chlorine in the effluent because after the initial dilution, the concentration of chlorine will be below water quality standards and will likely not be present at detectable levels once discharged”. A second report by Lavalli and Kropp (1998) examined and compared the densities of YOY and shelter-restricted juvenile lobsters at the proposed Mass Bay outfall site prior to the outfall activation. In early September 1998, suction sampling for YOY was conducted at both the vicinity of the outfall and two nearby inshore stations. The data collected showed significantly lower densities of YOY and yearling lobsters as well as larger early-benthic-phase lobsters at the outfall compared to the inshore sites. Lavalli and Kropp's report concluded that, “while the cobble habitat at the vicinity of the outfall is suitable for settlement, it does *not* represent a major settlement site and thus there is no indication that the outfall will have any appreciable impact on these life stages of the American lobster”.

Outfall benthic monitoring reports (dating back to 1992 and consisting of 23 fixed stations) concluded that associated hard-bottom communities have "not changed substantially with activation of the outfall" (Maciolek et al. 2009). MADMF (2010) indicated no short-term lethal effects on lobsters in the immediate environment surrounding the outfall. In addition, the report stated (at the time the assessment was conducted) that although isolated instances of chlorine exposure may adversely affect lobsters, this would likely be a discrete event in both time and space.

In terms of acute toxicity, Capuzzo et al. (1976) studied the effects of chlorine on larval (Stage I) lobsters in the laboratory and documented respiratory stress at levels of 5000 μgL^{-1}

of free chlorine and an LD_{50} of 16.3 mgL^{-1} (16,300 μgL^{-1}) of free chlorine (sodium hypochlorite) at 25°C. Additional LD_{50} tests at 20 and 30°C found no significant mortality at 20°C and exposure at 30°C resulted in an LD_{50} of 2.5 mgL^{-1}. Chloramines (post treatment residuals) and free chlorine was found to be harmful to Stage I larvae depending on the concentration, temperature, exposure duration and form of chlorine.

1.3.4. Commercial Fishing Practices

"Habitat alteration by the fishing activities themselves is perhaps the least understood of the important environmental effects of fishing" (NRC 1995). In order to help minimize adverse effects of fishing practices, the Swept Area Seabed Impact (SASI) model (and its parameters) was recently adopted to provide a coherent framework for "enabling managers to better understand the nature of fishing gear impacts (including lobster) on benthic habitats, and the spatial distribution of benthic habitat vulnerability to particular fishing gears" (see Figure 1 in NEFMC 2011). This comparative and integrative approach allows for a thorough assessment of gear types and their impacts and contributes to the objectives of essential fish habitat (EFH) in both New England and throughout the mid-Atlantic (NEFMC 2011).

Claw Loss & Shell Damage

Cull lobsters (those with missing or regenerating claws) are attributed to anthropogenic as well as natural causes. Among potential fishery-induced injuries, claw loss significantly impacts market value. Krouse (1976) calculated that cull lobsters weighed 14-20% less than fully clawed lobsters. Since 1999, an annual average of 10-20% of the total catch sampled from commercial lobster traps in Massachusetts coastal waters were culls (Glenn et al. 2007). However, an overlooked impact of culling is its effect in reducing the growth rate due to the energy partitioning between molt and regeneration (Aiken 1980). This can delay recruitment to minimum commercial size, and, if maturity is more a function of age than size, as it is in the spiny lobster (Davis 1981), then the size at maturity will be lowered. Claw loss can also affect lobster behavior. It is possible that since dominant lobsters "claim" the optimal shelters, animals which are behaviorally subordinate due to claw loss are forced to congregate on less optimal habitat (i.e., open sand or mud areas) which lack structure. Additionally, a number of lobstermen claim that there are areas that they refer to as "hospital grounds" where large numbers of culls can be found, particularly in estuaries (e.g., Moriyasu et al. 1999).

Inter- and intra-specific aggression in lobster traps, as well as handling by fishermen, contribute to claw loss which may also occur in the wild as a result of not only territoriality but through aggressive encounters as well (O'Neill and Cobb 1979). The relative contribution of each potential cause is unknown. Mobile gear fisheries contribute to lobster shell damage and can result in mortality. Observations of fresh shell damage and claw loss were made when investigating the impact of bottom trawling off Duxbury Beach, Massachusetts (Estrella 1989). The occurrence of fresh shell damage in new-shelled lobster was consistent with the results reported by Ganz (1980) in Rhode Island waters and Smith and Howell (1987) in LIS. Although Spurr (1978) did not record molt stage of the lobsters he studied off New Hampshire, he reported that the highest damage incidence occurred in July; when new-shelled lobsters are expected to be more abundant.

Trawling

Some level of delayed mortality occurs to new-shelled lobsters that are damaged by trawling (e.g., otter) and dredging (e.g., scallop). Smith and Howell (1987) observed delayed mortality in 33.3% of the 18 new-shelled lobsters they tested. Similar results were found by

Witherell and Howe (1989) who calculated a cumulative mortality of 29.5%. The mortality to undamaged hardshell lobsters was 0.6% (Smith and Howell 1987). The impact of trawling on sandy habitat is negligible and of short-term duration (Estrella 1989, Spurr 1978). Graham (1955) and Gibbs et al. (1980) found no detectable changes in benthic fauna as a result of trawling in their sandy study areas. Smith and Stewart (1985) concluded that no long-lasting impressions or habitat loss resulted from trawl door furrowing in soft mud bottom and only minor sediment disturbance (<1" depth) occurred in the sweep path.

More recently, Simpson and Watling (2006) conducted a study on the impacts of shrimp trawling in the GoM and its effects on mud-bottom fishing grounds. Their results suggest that seasonal shrimp trawling produced short-term changes (<3 months) to the macrofaunal community but did not seem to result in any long-term changes. Furthermore, the impacts to these trawling activities were mitigated, in part, by benthic megafauna (lobsters and fishes) through burrowing and pit digging by these animals; these activities acted to rework sediments thereby minimizing these impacts. It seems logical that lobster vulnerability should not be as great on rough rocky substrate where boulders would prevent the sweep from riding close to the bottom. Nocturnal vs. diurnal behavior may be important factors in lobster catchability from trawling. Smith and Stewart (1985) discussed the potential for greater lobster activity during daytime in dark deep-water environments compared to lighter shoal areas.

Traps

While there have been few studies on the effect of lobster traps on benthic habitats, available information suggests trap gear tends to have limited long-term adverse impacts on benthic habitat, particularly when compared with mobile fishing gears such as trawls and dredges. Because most inshore lobster traps are hauled, re-baited, and then reset on a regular basis, frequent hauling in areas of dense vegetation (e.g., kelp beds and eelgrass) is more likely to result in damage (ASMFC 2003, NMFS 2010). By comparison, the evaluation of lobster traps on attached epibenthic megafauna (sponges, soft corals, tube worms) in a European study showed no negative effect on the abundance of attached megafauna (Eno et al. 2001), however wind-driven effects on trap movements were shown to impact sessile benthic habitat fauna in the spiny lobster fishery (see Lewis et al. 2009). Therefore, variables such as depth, turbulence, and wind events may be factors that contribute to and influence trap-gear impacts. A workshop concerning the effects of fishing gear on marine habitats in the northeastern U.S. concluded that the degree of impact caused by lobster pots and traps to biological and physical structures and to benthic species in mud, sand and gravel habitats was low; impacts were expected to be greater in rocky habitats where emergent epifauna or biogenic structures are present (NEFMC 2002). More detailed work in this area could be useful in assessing *H. americanus* trap impacts to benthic habitat structure.

Ghost Traps & Derelict Gear

'Ghost fishing' can been defined as "the mortality of fish and other species that takes place after all control of fishing gear is lost by a fisherman" (www.fao.org/fishery) and can be detrimental to the lobster resource and its fishery. Ghost traps have been estimated to continue to fish at a rate of 10% the effectiveness of a baited trap with 25% of the ghost trap lobsters dying (Pecci et al. 1978) and represents an ~3-6% loss in annual landings in the U.S. (Harding 1992). Regulations addressing ghost fishing through a requirement of biodegradable escape panels or hinges are now in place in most states however it is important to note that few studies have been carried out to assess the degradation time for these devices (although they are usually replaced annually, C. Wilson, pers. comm.). Lobsters and other marine animals captured in derelict traps may experience starvation, cannibalism, infection, disease or prolonged exposure to poor water quality (low dissolved oxygen, Guillory 1993). In the Chesapeake Bay blue crab fishery, Havens et al. (2008), used side scan sonar to locate derelict traps and assess their extent and accumulation rate in the York River, Virginia. Trap loss rates were estimated at 30%, resulting in the potential addition of over 100,000 traps annually to the Chesapeake Bay derelict trap population in Virginia.

Gear loss can be expensive (~$100 per trap) and with the advent of inexpensive and readily available technology such as GPS systems, the retrieval of lost gear is possible. In other instances, programs have been carried out to recover, document and dispose of derelict (ghost) lobster traps (Gulf of Maine Lobster Foundation, GOMLF, 2011, see http://www.gomlf.org/index.asp). For example, during the 2010 gear recovery effort, more than 1,000 traps were recovered by 27 fishing vessels from three lobster conservation management zones. In WLIS, the Cornell Cooperative Extension (CCE) conducted a total of 28 research trips during the Fall of 2010 and retrieved 2,298 derelict lobster traps and recycled 25.95 tons (51,900 lbs.) of derelict lobster traps into clean renewable energy (CCE, NFWF 2012). The CCE study also catalogued each trap that was retrieved (e.g., physical condition, escape vent present) and concluded that these abandoned, lost, or discarded lobster traps are a problem in WLIS. Often, many of the LIS lobster traps that were recovered had sunk into the mud above the vent, making them inoperable. Similar efforts have also been underway (in LIS) through the National Fish and Wildlife Foundation's WLIS Marine Debris Assessment and Prevention Program (NFWF 2012).

Between 2010 and 2011, a series of 'abandoned' lobster pot trawls were deployed and monitored (SCUBA assessments) in Cape Cod Bay and Buzzards Bay. A key finding from this study showed that ghost traps continue to fish for longer than previously thought (> 2 years or more; NFWF 2012). Additionally, traps that are set in deeper waters or in proximity to sheltered environments "may continue to catch lobster and bycatch species for an extended period of time due to a lack of oxidation of the metal (hog rings) while in the water and attachment of biofouling organisms over the escape panels"(NFWF 2012).

Whale Entanglements

Although a variety of species are potentially capable of entanglement from lobster trap gear, whales (in-particular North Atlantic right whales, but others as well) are vulnerable due to their propensity to feed below the surface, or feeding while swimming with their mouths open (NMFS 2010). Johnson et al. (2005) noted that any part of the trap gear complex (the buoy line, ground line, float line, and surface system line) creates a risk of entanglement. It is probably the case that the total numbers of entanglement are greater than those actually recorded. For example, a total of three right whale entanglements due to lobster gear were documented in Maine coastal waters between 1997-2005 (NMFS data compiled by the Massachusetts Lobstermens Assoc.), and 48 cases of entanglement from 1997-2005 in Northeastern waters (NMFS compilation for ALWTRT). Additional studies concluded that 60% and 70% of right whales exhibited entanglement scarring, suggesting this is an ongoing issue (Fujiwara and Caswell 2001, Myers et al. 2007). The problem seems to be more significant in offshore waters where vessels tend to fish larger strings of traps. Although Federal regulations seeking to mitigate entanglements by mandating sinking ground line on all lobster trap gear (effective April-2009), vertical lines that link the bottom-tending trap to the surface line(s) and buoy(s) continue to pose an entanglement risk to protected species (NMFS 2010).

Bycatch

The term 'bycatch' refers to the unintentional landing and discarding of animals not specifically targeted by fishing vessels (NMFS 2010). In general, traps used in commercial lobster fisheries are among the more selective types of fishing gear but they are known to capture non-targeted species. Therefore, bycatch is a relevant and indirect component to habitat since there is the potential to alter community structure (e.g., removal of predators). By and large, overall levels of bycatch in lobster traps are low relative to other marine fisheries. Fish and invertebrates landed in lobster traps are likely to be discarded with lower mortality rates than those landed with other gear types such as trawls and dredges (Davis 2002).

Fishes that are caught in lobster traps include tautog, scup, black sea bass, cod, cusk, eels and flounder. C. Wilson (data from Maine DMR) indicated that at least 10 finfish species are routinely documented as discarded bycatch (see Table 1 in Bannister et al. 2013). The most abundant fish bycatch is longhorn sculpin, comprising 0.5% of the lobster catch over a 3-year period. In addition to fish, a variety of invertebrates are found in and attached to lobster traps, including Jonah and rock crabs, red crabs, starfish, urchins, whelks and conchs (ASMFC 1997, Bannister et al. 2013). The discard mortality rates (% of discarded animals that die) associated with animals caught in traps is considered low, particularly when compared against the mortality rates linked with mobile fishing gears such as trawls and dredges (NMFS 2010).

Lobster Trap Bait

Bait used in lobster traps is an important component of the lobster fishery. It has been estimated that 50-60,000 tons of bait (primarily Atlantic herring) are used in the U.S. lobster fishery annually (NMFS 2010). In Maine, herring comprises nearly 90% of the bait used while in SNE, skate (~ 15,000 tons/year since 2001) are frequently substituted as bait. Many lobstermen consider the amount of bait being used in the fishery as providing a positive effect on the lobster population as it is often remarked that 'lobsters are being farmed'. The rationale behind this notion is that sub-legal sized lobsters, in addition to other bycatch (fishes and crabs), move in and out of traps to feed on bait. Thus, this 'bait subsidy' (bait use has increased 4-fold since the 1970s in Maine) is responsible for an increase of lobster abundance in some areas and may be a contributing factor in lobster biomass in some coastal areas (Grabowski et al. 2009, 2010). In one recent study, Grabowski et al. (2009) determined that sublegal lobsters in midcoast Maine grew 15% more per molt in fished areas (with trap bait) compared with closed areas, suggesting an effect of the bait subsidy; however at another site in eastern Maine, lobsters at unfished sites grew faster than those at fished sites. The differences in natural diets between sites confound these results indicating the challenges in controlling these effects in the wild.

In terms of bait utilization, it has been suggested that that about 2/3 of bait in traps is used by lobsters and the remaining 1/3 by crabs and other species (Grabowski, pers. obs.). It is proposed that bait may comprise a large proportion of a lobster’s diet (upwards of 34-55 %), which could substantially impact their overall health as well (Myers and Tlusty 2009). A recent survey of bait use by Nova Scotian lobstermen indicated an average of 860 g (1.9 lbs.) of bait (herring or mackerel) was used each time a trap was set, translating to over 5,216 kg (11,500 lbs.) of bait/year/lobsterman (Harnish and Willison 2009). With such large volumes of bait being used in some areas, the ecological and economic implications of bait subsidies may be a concern to both scientists and industry.

1.4. Climate Change Impacts to Lobster Habitat Components

Climate change has always been an integral part of natural ecosystems and the fisheries that are supported therein. Although many fisheries worldwide can be resilient to environmental changes (Brander 2009), some factors may in fact limit this capacity: 1) the rate of climate change is predicted to accelerate in the near-future; 2) resiliency in species and systems is being compromised by increasing fishing pressures, pollution, habitat degradation, disease, and invasive species; and 3) the effects of lowering of the oceans pH due to rising CO_2 levels remains mostly unknown (Brander 2007, 2010). Additionally, distributional shifts to higher latitudes and deeper waters of commercially important marine species (including lobsters), in response to warming temperatures is leading to changes in community structure, trophic interactions, and the dynamics of fisheries, with increasing vulnerability of many coastal fisheries to climate change (Pinsky and Fogarty 2012, Cheung et al 2013).

Given the highly influential role that temperature has on all life history phases of *H. americanus* (Fogarty 1995), and the sensitivity of lobster growth and reproductive dynamics to variations in temperature regimes (Waddy and Aiken 1995), it is not too hard to prognosticate how climatological changes could affect lobster broodstock fecundity, size at maturity, egg development, and hatch, species range and distribution, population densities, among others. For example, rising seawater temperatures would accelerate egg development and hatching, thereby shortening larval development. In some areas, offshore movements by lobsters seeking to avoid warm water could cause eggs to hatch too far offshore (Goldstein 2012, Pugh and Glenn 2012), setting up sub-optimal dispersal trajectories and possible larval wastage. Other climate-related scenarios are certainly possible as well.

Changes in ocean temperatures will undoubtedly cause alterations to thermal profiles that would have cascading effects on the movement dynamics of ovigerous lobsters, which in turn, would influence egg development rates, timing of hatch, predation and ultimately, larval survivorship and dispersal. Continued and more detailed investigations of the physiological tolerances, thermal thresholds, and behaviors of ovigerous lobsters, their eggs and larvae and would certainly contribute to further enhancing our knowledge-base of the effects of changing ocean temperatures.

1.5. Present Condition of Habitats and Habitat Areas of Particular Concern (HAPCs)

American lobsters utilize and reside in nearly all habitat types throughout their range. This includes estuaries, intertidal zones, coastal nearshore waters, and offshore banks and deep-water canyons (Factor 1995, Lincoln 1998). NMFS (2010) report Table 3.13 describes in-detail these habitats and their characteristics. Habitat Areas of Particular Concern (HAPC) are described as subsets of Essential Fisheries Habitat (EFH) which are rare, particularly susceptible to human-induced degradation, especially ecologically important, or located in an environmentally stressed area. Although there are currently no documented HAPCs for American lobster, some areas that are particularly vulnerable to protracted and well-documented hypoxia events (LIS, Pearce and Balcom 2005), sub-optimal water temperatures (Buzzards Bay and other areas of SNE and LIS, Pearce and Balcom 2005, Pugh and Glenn 2012) and the presence of deleterious compounds in sediments, certainly warrant consideration for the survival of some lobster populations.

There are anecdotal reports from fishermen of habitats that, at certain times of the year, are spawning and broodstock habitats for ovigerous females. Lobstermen, usually try to avoid these areas, however large numbers of broodstock lobsters that do get caught may be subjected to rough handling practices. While the identification of these ‘brooding areas’ is known for some crab species (Dungeness crabs, Stone and O’Clair 2002), it is not documented for ovigerous American lobsters. It is essential that identified broodstock and nursery areas are prioritized habitats for lobsters. Finally, because we know that lobsters do in fact populate estuarine systems with regularity (and are purported to reproduce and possibly settle there (e.g., Wahle 1993, Goldstein and Watson unpub. data), these habitats are of particular concern given their pronounced vulnerability to habitat degradation and climate change (Kennish 2002).

1.5.1. American Lobster Habitat Bottlenecks

The ASMFC Habitat Guidance Document (2013, pending approval) defines a habitat bottleneck as “a constraint on a species' ability to survive, reproduce, or recruit to the next life stage that results from reductions in available habitat extent and/or habitat capacity and reduces the effectiveness of traditional fisheries management options to control mortality and spawning stock biomass.” Although there is some evidence of preferred habitat types (both physical and biological, see Section 1.4.1 for review), there is no concrete supporting evidence that habitat is currently limiting to populations of American lobster. However, there are scenarios affecting components of lobster habitat (i.e., thermal) that would suggest otherwise. First, the “confluence and succession” of environmental factors that provoked a catastrophic loss in the LIS lobster population in 1999 (see Pearce and Balcom 2005 for summary), creating limited areas where lobsters could find safe refuge (although 90% were unable to do so). These lobsters, already compromised by disease (parasitic amobae), and above average water temperatures, became "physiologically weakened", resulting in significant population losses (CTDEP 2000). Therefore, selected habitat combinations that become stressful to lobsters (temperature, dissolved oxygen) can leave some populations vulnerable to further disease and possibly limit areas where conditions are more favorable to survival.

A second scenario involves the contraction of optimal or useable thermal habitat by lobsters (for basic physiological processes, egg and larval development, and growth) and is exemplified by seasonal changes and conditions in bays and estuaries where temperatures become sub-optimal for lobsters at certain times of the year. Repeated studies in Great Bay Estuary (NH) and Narragansett Bay (RI) have convincingly shown that lobsters will selectively avoid areas of sub-optimal temperature (e.g., excessively warm, in summer; Howell et al. 1999, Jury and Watson 2012, MADMF data). As a result of these differences, estuarine systems can become bottleneck habitats if conditions in these areas continue to deteriorate over time. Historically rich lobster populations such as in Buzzards Bay have now experienced dramatic declines and experience summertime temperatures in excess of 20°C (MADMF data, Pugh and Glenn 2012). As a result, lobsters have been concentrated at the mouth of the Bay. Recent MADMF data suggests that lobsters (including ovigerous females) are moving to deeper, cooler waters, thereby concentrating their populations in a much smaller area. These kinds of ‘thermal refuges’ may become increasingly common and create potentially significant bottlenecks with respect to brooding areas, places for lobsters to shelter and even possibly altered larval dispersal due to differences in their movements.

1.5.3. Habitat Enhancement

Due to past and present adverse impacts from human activities, restorative projects appear likely to have slightly positive effects at the local level. There have been few documented examples of lobster habitat enhancements in the GoM, but there may be significant potential for more, including the planting of artificial kelp beds (NMFS 2010). Artificial shelters made of PVC pipe and concrete blocks were have also been used with good results (Ojeda and Dearborn 1991). So far, evidence seems to indicate that these methods merely serve as gathering points for lobsters in the surrounding area (i.e., the 'attraction hypothesis'), leading some to believe that overall lobster density is not necessarily increased. However, in at least one study (Barber et al. 2009) it has been shown that early-benthic lobster settlement does in fact occur on some artificial reefs.

A number of studies have suggested that, in some areas, shelter is a limiting factor in the distribution and abundance of nearshore lobsters (Butler and Herrnkind 1997 for spiny lobsters, Whale and Incze 1997 in clawed lobsters). The addition of artificial reefs in areas previously devoid of cover or substrate suitable for burrowing has been shown to increase the abundance of resident lobsters (reviewed in Sheehy 1982). Observations have also indicated that extensive growth of encrusting organisms on artificial substrates serves as a source of food for lobsters. Following the M/V World Prodigy oil spill, NOAA and the University of Rhode Island (URI) designed and established an artificial reef system to increase lobster (www.darrp.noaa.gov.html). A total of six cobblestone reefs (in ~15 ft. of water) in Dutch Island Harbor near Jamestown, Rhode Island, were constructed to provide shelter for lobsters of all sizes. In 1997 more than 2000 tagged hatchery-reared YOY lobsters (Stages V-VI) were released over two successive years. Although the settlement of YOY lobsters was significantly increased, the density of YOY lobsters on enhanced reefs was not different from that on the control reefs; further results indicated possible behavioral differences between hatchery-reared lobsters making them more susceptible to predation (Castro et al. 2002, Castro and Cobb 2005). Therefore, future restocking efforts should focus on the behavioral conditioning of hatchery-raised lobsters in order to provide the best chances for survival.

An alternative approach to artificial reef development was recently developed and utilized to focus on criteria that would presumably make for a successful artificial reef for the settlement and growth of lobsters. Barber et al. (2009) developed a series of seven selection factors ('exclusion mapping, depth and slope verification, substrate assessment, data weighting and the subsequent ranking analysis, visual transect surveys, benthic air-lift sampling, and larval settlement collector deployment') that were used to model the efficacy, design, and implementation of an artificial reef system for lobster as related to the best possible biological and physical attributes, including a natural supply of larvae. Within only a short time post installation did this artificial reef yield densities of invertebrates and YOY lobsters that were similar to nearby natural reefs, suggesting that these structures may have future applications.

1.6. Recommendations for Further Habitat Research

Throughout this section there are already many mentioned areas that warrant further detailed research. Below is a thematic list of research topics pertaining to lobster habitat components where data gaps exists or areas where only limited evidence is currently available.
Environmental variables: How is this habitat component related to depth and temperature? They are often related, but it remains difficult to ascertain if lobsters are moving or choosing an area because of the depth or the habitat. Also, do lobsters aggregate in areas with their

‘preferred’ temperatures? Although there is already evidence for this (e.g., Crossin et al. 1988), we do not know how widespread this occurs. How would anticipated climate change scenarios (temperature, acidification – pH, sea level rise, and salinity) influence lobster life-history processes? For example, given changes to the Gulf of Maine current regime, how might egg development, larval duration, and larval transport become altered?

Ocean Acidification (OA): This is clearly a specific environmental variable we have very limited information regarding American lobsters. We can draw on only a few examples of other marine decapods (crabs, summarized in previous section) but studies that include all life-stages of lobsters should be considered. Focal questions could address how OA might affect larval development and growth, shell integrity in juveniles and adults, and even possibly behavioral changes.

Traps: There is much to learn with respect to trap dynamics – how effective are traps to the sheltering and/or aggregation effect? Also, the dynamics of bait consumption and bycatch as well on lobsters is also relevant. Related to this are the impacts of bait consumption on lobster physiology and health. Although some recent study efforts have been carried out, we need to get a much better handle on ghost trap dynamics and how to quantify their impact.

Lobster Movements: There are many questions here that can be asked in the context of a changing ocean climate. For example, what environmental trigger(s) motivate lobsters to move offshore? Is it only based on temperature? What advantages are there for lobsters to move offshore and how have these patterns changed in specific regions of the fishery? Does shelter quality (or lack thereof) instigate movements to other areas? Based on previous findings from WLIS and Buzzards Bay, what are the 'threshold factors' that elicit lobsters to move away? What combinations of environmental factors and minimal levels are detrimental? Some recent work has suggested that some lobster movement may involve orientation along specific benthic habitat types suggesting habitat corridors of movement in some cases. This is one area of research that should be expanded upon as well.

Finally, do lobsters move and shift their habitats in anticipation of critical events like molting (finding a safe place to molt)? Furthermore, what about the importance of certain habitat types when lobsters densities become too high? – Will lobsters ‘spill over’ into poor habitat? One important, but sometimes controversial topic is the efficacy of marine protected areas for lobsters. Identifying habitat areas that are integral for brooding aggregations may be a useful starting point.

Mapping & Settlement: The mapping, characterization, and quantification of lobster habitat types needs to be continued throughout U.S. waters. The identification of habitat important to postlarval settlement and early benthic phase lobster is necessary in order to calculate a density index and evaluate a stock-recruitment relationship. Changes in species composition by area, from a hard-bottom complex to a soft-bottom complex and prey diversity on each bottom type should be determined. This information is an important precursor to recruitment assessments and to mobile gear impact studies.

Because, it was recently shown that postlarval lobsters can in fact settle in deeper waters, how common is this and do lobsters routinely settle offshore?

1.7. Recommendations for Monitoring and Managing Lobster Habitat

Most of the current management measures today (minimum sizes, v-notching, closed season, maximum size, slot limits, trap limits, protection of ovigerous lobster) were either discussed or implemented over 100 years ago. Many if these do not include habitat considerations and as such have had very mixed success. In order to be effective, both in supporting sustainable lobster stocks and viable harvest fisheries over an extended geographic range, new analyses of trends in lobster distribution must include known linkages of lobster survival and growth with threshold environmental conditions. Assessment models should incorporate climatic variables such as sea temperature, dissolved oxygen, and salinity by including these drivers as model covariates. To support these necessary modeling exercises, it is important to develop and maintain consistent techniques that monitor distribution and abundance of lobster independent of the fishery so that lobster populations and their habitat needs can be effectively managed throughout their range.

Of particular importance is the need to continue and expand monitoring of the young-of-year and larval production so that highly productive areas are identified and protected. The last stock assessment peer reviewers emphasized the importance of monitoring recruitment in a fishery that relies heavily on newly-mature animals. The early benthic shelter-seeking phase may be the most habitat-dependent and therefore may form the most critical bottleneck determining ultimate population survival rates.

Some suggestions for monitoring the Southern New England lobster stock are outlined in the October 2011 peer review of the ASMFC Lobster Technical Committee Report entitled *Recruitment Failure in the Southern New England Lobster Stock*. One suggestion is for lobster surveys to be continued, and if possible increased, in the future to "enhance their power to detect changes in larval or young-of-year abundance." New surveys should be developed to give a more spatially comprehensive view of spawning patterns possibly with the deployment of passive postlarval collectors. Such surveys should be used to improve the understanding of the recruitment processes, provide early feedback on the success of management measures aimed at protecting spawning habitat and potential, and to allow forecasts of recruitment for both inshore and offshore areas.

Regionally, in the at the southern end of the current lobster distribution the combination of hypoxia and rising water temperature is narrowing the habitat area which can support a healthy lobster stock; identifying areas meeting minimum requirements (>2 ppm DO and <20° C) on an annual basis may provide guidance for stock rebuilding efforts.

The Southern New England Management Area (SNE) for American lobster is experiencing a general decrease in population abundance, particularly in the northern reaches of the range; Lobster Conservation Management Area (LCMA) 2, 4 and 6, as well as adjacent offshore areas of LCMA 3. Much of what is known about these areas has come through efforts made by the bordering states through ventless trap surveys, larval settlement surveys and continuous environmental data collected through fixed buoy systems for both surface and bottom temperatures. Before 2008, little work was completed in LCMA 4 and 5 when the New Jersey at-sea observer program started. New Jersey has been able to collect valuable fishery characterization data but lacks any serious effort at answering questions regarding juvenile habitat and recruitment areas. In order to complete the coverage of the SNE range, fishery-independent surveys in this area are critical.

The Gulf of Maine is a semi-enclosed marginal sea with several deep basins, strong tidal currents and a generally cyclonic circulation. Scotian Shelf water enters along the south coast of Nova Scotia and exits primarily along the northern edge of Georges Bank and secondarily through the Great South Channel (Brooks 1985). Currents are necessary for larval lobster transport that links inshore (coastal) and offshore (basin) lobster populations. Fogarty (1998) calculated that a modest amount of offshore larval supply could add significantly to resiliency of populations in inshore areas where the fishery is concentrated. Favorable conditions for larvae can greatly increase development rate and when coupled with typical physical forcing factors observed within the Gulf of Maine, as described above, create a delivery mechanism of competent larvae to nearshore nursery grounds (Incze and Naimie 2000). These favorable habitat conditions should be assessed and monitored as climatic variables may alter the success of this mechanism in future years.

Clear communication and cooperation among partners, agencies, councils, etc. that manage other fisheries can be an effective tool in maintaining productive American lobster habitat. An example would be conducting surveys to determine the distribution of critical life stages of lobster prior to the opening of areas closed to particular fisheries which may affect lobster habitat. Data from such surveys would inform managers of critical times and habitats vital to lobster growth and reproduction in the area. Periodic or rolling closures have proved to be very effective management strategies when the requirements of all marine resources are well known and well met.

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