LOBSTERS ON THE EDGE- ESSENTIAL LOBSTER HABITATS IN NEW ENGLAND

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EXECUTIVE SUMMARY

This report combines up-to-date information on lobster biology and ecology with oceanographic and geological data in order to define Essential Lobster Habitats. The following preliminary report and maps update knowledge of the marine bottom sediments in the Gulf of Maine region and combine this with the distribution of lobsters found in NMFS trawl data. Additionally, surface temperatures, current patterns and water masses have been defined from satellite data and combined with lobster distribution patterns where possible.

While the physical tolerances of the American lobster have been studied for more than a century, the lobster's habitat preferences have only recently been explored. Modern experiments with state-of-the-art techniques have given us entirely new insights into the optimal conditions sought by the lobster. With this in mind, lobster life-stages are described in detail and inferences are made about shelter requirements and dependency during various growth phases. Known or suspected lobster habitats are reviewed and evaluated. Where possible, an estimate has been made of lobster density for each life stage.

The literature suggests that lobsters are highly dependent on natural shelters for some period during each stage of their life cycle. The young must find coarse sediments for settlement in order to avoid predators. They must continually find or create new shelters as they molt and grow. Mature lobsters continue to need shelter protection during molting and also to facilitate reproduction. Many large male lobsters apparently have difficulty finding a mate without suitable mating shelters. This places an extraordinary burden on lobsters to locate and defend shelter-providing habitats. Additionally, some large females are unable to reproduce without the availability of large males.

While inshore lobsters have been reported on nearly every substrate, they appear to be concentrated near cobble or rocky shorelines and around island margins and estuaries. Offshore lobsters tend to focus along relatively narrow bands at the edge of the shelf and possibly close to the transitions from one habitat to another.

Until such time as accurate maps can be generated of total lobster distribution, we can only approximate how lobsters utilize various habitats. However, given the definitions of Essential Fish Habitat (*waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity*) and the identification of the most vulnerable habitats of these habitats (where vulnerability is based on *the extent to which the habitat is sensitive to human-induced environmental degradation; whether, and to what extent, development activities are, or will be, stressing the habitat type, and the rarity of the habitat type*), we have identified the following habitats as those both utilized by lobsters, important to the completion of their life cycle, and sensitive to human activities:

> **Rock, Cobble and Gravel** - These habitats represent critical nursery grounds (postlarvae, juveniles, adolescents) for the American lobster and should be given a high priority, particularly given the location of these beds and the impact that near shore human activities can have on them.

Peat Reefs - All life stages have been reported, with shelter-restricted and emergent juveniles most common; thus may also be an important nursery ground when cobble is lacking. Since these reefs are part of wetlands, they have a great potential of being impacted by human activities and should be considered a vulnerable habitat.

Island Margins - All life stages seem to be present at these margins.

Kelp Beds - These habitats may represent important grounds for the more vagile adolescents.

Eelgrass Beds - The regional importance of eelgrass beds as a lobster habitat appears to be minor, but adequate studies are still lacking. Until more is known, and according to the conservative approach adopted by NMFS, they should probably be considered Essential Lobster Habitat. Futhermore, human activities have negatively impacted eelgrass beds in the past and can continue to do so, making them a particularly vulnerable habitat.

Intertidal Zone - Given the fact that shelter-restricted, emergent, and vagile juveniles have been found in this habitat in 5 New England states, NMFS should probably adopt a conservative approach here and declare it as a potential nursery ground and Essential Lobster Habitat. The intertidal zone also has one of the greatest potentials to be strongly impacted by human activities and should be considered vulnerable.

Bedrock Base with Rock and Boulder Overlay - An important and probable Essential Lobster Habitat for vagile juveniles, adolescents, and adults. May be vulnerable to certain fishing practices.

Offshore Sand Base with Rock - This substrate type is not very common offshore, but is almost certainly an Essential Lobster Habitat for all life stages. It too may be vulnerable to certain fishing practices.

Clay Base with Burrows and Depressions - Apparently this substrate is depth-restricted, but is a probable Essential Lobster Habitat for adolescents and adults.

Mud-Clay Base with Anemones - An extremely fragile environment which is also severely depth-restricted. It is a strong candidate for an Essential Lobster Habitat for adolescents and adults and is extremely vulnerable to fishing activities because of its fragility.

Clay Pipes - There have been numerous anecdotal reports of clay pipes serving as lobster habitat and until more is known, NMFS should adopt a conservative approach to their protection, particularly given their rarity.

Submarine Canyons - The offshore submarine canyons represent a particularly important habitat for abundant adolescent and adult lobsters, ovigerous females that may be hatching their eggs, and may be one source of larval supply. As such, they should be protected as an Essential Lobster Habitat.

Two other habitats which should be considered as potential Essential Lobster Habitat are Mud-shell/rock substrate and Mud base with burrows. However, these habitats are less important than those listed above, given the lower densities of lobsters found on them.

By protecting Essential Lobster Habitats which offer optimum conditions for growth and reproduction we can, perhaps, perpetuate a strong and viable lobster stock.

Essential Habitats for Lobsters

An essay for management considerations by:

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Growing concerns about the preservation of exploited marine species has lead to the inclusion of "essential habitat" considerations in recent Federal legislation included in the Sustainable Fisheries Act. This has caused some confusion about what essential habitat is and how it can be effectively managed. Essential habitats need to be, defined for each managed species to be useful. Without such definitions, anywhere an organism is found or could be found might qualify as an essential habitat. We believe that it might be useful to prioritize the importance of specific habitats so management actions for their protection can be applied "surgically". Specifically we note that specific phases during the life history of lobsters require specific habitats and such linkages have a disproportionately great impact on lobster populations. In our view such habitats should be given priority for protection and considered as "essentia1 habitats".

Below we will define our terms, articulate the logic of our conclusion and suggest a means of proceeding while science continues to fill gaps in our understanding about the biology of this species..

"Habitat" is where an organism lives. "Essential habitats" are places that have a disproportionately great impact on an organisms abundance during some critical phase in their life cycle. A "critical phase" for an organism is the period in its life when it is most susceptible to mortality or, for other reasons (e.g., spawning), has a disproportionately great influence on population size. For many marine organisms this period occurs at the time of settlement as they make the transition from their planktonic (floating) larval life to bottom-dwelling life (Doherty and Fowler 1994). The duration of this critical phase, however, can vary and may not exist for some species (i.e., there may be no developmental change in vulnerability as some organisms mature, especially very small organisms).

Some organisms require a specific habitat at a critical phase in their life. Such habitats are generally called "essential". The linkage between a species and a specific habitat may functionally control the carrying capacity of the environment for that species. For lobsters, there is considerable research suggesting habitats supporting broodstock lobsters and those that serve as nursery grounds are most essential. We hasten to add that this does not mean that habitats where juvenile lobsters grow are unimportant, only that we know of no studies that show population declines (that is lobsters die) when juvenile habitats are lost.

Broodstock habitats include spawning areas and habitats lobsters use while their eggs develop externally on their abdomen. Rough handling during this phase can cause spontaneous abortion. Broodstock lobsters are most abundant in deep water and off shore locations especially in the winter but their exact habitats are unknown. In some locations, gravid females are known to migrate to shallow water during the summer (Campbell 1986) but the generality ofthis phenomena is not yet known.

Lobsters select specific nursery grounds for settlement and studies have shown that their survivorship is greater in nursery grounds having specific architectural characteristics (Hudon and Lamarche, 1989; Wahle and Steneck 1991, 1992, Wahle 1992). All known nursery grounds (i.e., microhabitats where post-settlement survival is high) for lobsters contain small shelter providingspaces. In areas around Cape Cod, vegetation root mats have been shown to harbor newly settled lobsters. In many regions throughout coastal New England, cobble-stones contain the greatest densities of newly settled lobsters (Wahle and Steneck 1991, Cobb and Wahle 1994, Incze et al. 1997, Palma et al 1998). Newly settled lobsters remain near their settlement site for the first several years, rarely venturing out of the nursery habitat. They probably sustain themselves during this phase by feeding on plankton drifting by and through their micro-shelters (Lavalli and Barshaw 1989) as well as benthic organisms found in the immediate vicinity of their shelters. Recent studies have shown that lobster settlement is largely limited to water shallower than 20 in (Wilson and Steneck in prep). Moreover, cobbles and boulders comprise only about one-eighth of the shore of the Gulf of Maine, and an even smaller fraction in deeper waters or along shores to the south (Kelley 1987, Wilson and Steneck in prep.). These shallow, densely populated lobster nurseries should be priority essential habitats for protection.

While broodstock and nursery habitats are priority "essential habitats" for lobsters, there are other potentially important phases for which we know too little. Because lobsters need habitat for spawning and nursery grounds to be safe from predators, we suggest those refugia are the most important "essential habitats".

We offer our thoughts to indicate how we weigh the importance of specific habitats at specific life history phases of lobsters. We do this fully realizing these issues are not black and white. Perhaps by prioritizing habitats as we have, we may give the clearest guidance currently possible for management action. Our collective opinion reflects the current state of the science but it is not, and should not be the final word.. If we follow a framework for protecting regionally significant habitats (Steneck 1995, Langton et al 1996), we must be prepared to test the assumptions we have put forward and to periodically reconsider them as prescribed in the practice of adaptive management

Literature Cited:

Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. Can. J. Fish. Aquat, Sci. 43: 2197 - 2205.

Cobb, S., Wahle, R. 1994. Early life history and recruitment processes of clawed lobsters. Crustaceana 67: 1 - 25.

Doherty, P., and Fowler, T. 1994. An empirical test of recruitment limitation in a coral reef fish. 1994. Science. 263: 935 - 939.

Hudon, C., Lamarche, G. 1989. Niche segregation between American lobster, *Homarus americanus* and rock crab *Cancer irroratus*. Mar. Ecol. Prog. Ser. 52: 155 - 168.

Incze, L. S., Wahle, R. A. and Cobb, J. S. 1997. Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus*. Mar. Freshwater Res. 48: 729 - 743.

Kelley, J. 1987. Sedimentary environments along Maine's estuarine coastline. In: FitzGerald, D. M.,

Rosen, P. S. (eds) A treatise on glaciated coasts. Academic Press, New York, p. 151 176.

Langton, R., R. Steneck, V. Gotceitas, F. Juanes, P. Lawton. 1996 The interface between fisheries Research and habitat management. North American Journal of Fisheries Management. 16: 1 - 7.

Langton, R., R. Steneck, V. Gotceitas, F. Juanes, P. Lawton. 1996. The interface between fisheries research and habitat management. North American Journal of Fisheries Management. 16: 1 - 7.

Lavalli, K. L., Barshaw, D. E. 1989. Post-larval American lobsters (*Homarus americanus*) living in burrows may be suspension feeding. Mar. Behav. Physiol. 15: 255 - 264.

Palma, A. T., Wahle, R. A. and Steneck, R. S. 1998. Different early post-settlement strategies between American lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) in the Gulf of Maine. Mar. Ecol. Prog. Set. 162.215 - 225.

Steneck, R. S. 1995 A framework for protecting regionally significant habitats: environmental science considerations. Pages 147 - 152 in Proceedings Nationa1 Research Council Symposium: Improving the Interaction between Environmental Management and Coastal Ocean Sciences. National Academy Press. Washington, D. C.

Steneck, R. S., Langton, R. W., Juanes, F., Gotceitas, V. and Lawton, P. 1997 The interface between fisheries research and habitat management: Response to comment. North American Journal of Fisheries Management. 17: 596-598.

Wahle, R. A. 1992. Substratum constraints on body size and the behavioral scope of shelter use in the American lobster. J. Exp. Mar. Biol. Ecol. 159: 59 - 75.

Wah1e, R. A. and R. S. Steneck. 1991 Recruitment habitats and nursery grounds of the American lobster (*Homarus americanus* Milne Edwards): A demographic bottleneck? Marine Ecology Progress Series. 69: 231 243.

Wahle, R. A. and R. S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. Journal of Experimenta1 Marine Biology and Ecology. 157: 91 - 114

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1). PURPOSE

The purpose of this report is to define areas that could eventually be designated as Essential Fish Habitat (EFH) for American lobster. This EFH designation is mandated by Congress for all managed species by the Magnuson-Stevens Act which was amended in 1996 under the Sustainable Fisheries Act (SFA). Essential Fish Habitats must eventually be defined by the councils and the National Marine Fisheries Service (NMFS). By completing this report before the congressional deadline of October 1 1998, an opportunity exists to enlist the cooperation and support of lobster harvesters, dealers and organizations, all of whom stand to benefit from an objective review of existing scientific data.

Without a definition to be considered by the Council, the impact of each of the other fishery management plans on Lobster Habitat cannot be assessed. This report presents the facts that will have to be considered by NMFS in order to comply with the SFA. The integration of this scientific data will, hopefully, help to guide and influence the EFH process by ensuring the long-term health and survival of both the American lobster and the lobster industry

2). SCOPE

This study pulls together data relevant to the delineation of lobster habitats throughout the NW Atlantic region (Fig. 1) in both state and federal waters of the United States (Fig. 2). The goal is to consolidate basic scientific information and recent research on bottom sediments, rock types, and water conditions with lobster biology. This report is the result of an extensive review of the literature as well as existing maps and charts that could shed light on American lobster ecology. Every effort was made to include the latest scientific findings and maps (even if preliminary or unpublished) in order to take full advantage of the current state of knowledge in the lobster field. In addition, input from lobster fishermen up and down the New England Coast was solicited in an effort to include their experience in the pool of available resources.

3). INTRODUCTION

Nearly one hundred years ago, Francis Herrick, one of the pioneers in the study of *Homarus americanus* (hereafter referred to by its common name, American lobster), remarked, "in all probability there is no marine invertebrate in the world which is better known" (Factor 1995). Since that time, the studies of this species have expanded tremendously and his statement is even truer today. There are hundreds of research papers which deal with lobster ecology alone. Any attempt to digest this vast literature is a difficult task and it would not be possible without the thorough and comprehensive reviews of previous workers. Most notable in this regard is the excellent two volume set edited by Phillips and Cobb (1980) entitled "The Biology and Management of Lobsters" and the superbly illustrated work edited by Jan Robert Factor entitled "Biology of the Lobster" (Factor 1995). Recent research by scientists and students at the Darling Marine Center (University of Maine), Bigelow Laboratory for Ocean Sciences, University of New Hampshire, University of Rhode Island and others have added immeasurably to our basic understanding of lobster requirements. Yet, despite the efforts of these dedicated researchers, there are still fundamental questions about lobster ecology which remain a mystery.

4). DEFINITIONS

According to the Magnuson-Stevens Fishery Conservation And Management Act (Public Law 94-265) as amended through October 11, 1996 hereafter referred to as the **Sustainable Fisheries Act (SFA)**, the following definitions appear:

(SEC. 3. DEFINITIONS 16 U.S.C. 1802)

- **Fish-**

99-659, 101-627

(*12) The term "fish" means finfish, mollusks, crustaceans, and all other forms of marine animal and plant life other than marine mammals and birds.*

- **Essential Fish Habitat**-

104-297

(*10) The term "essential fish habitat" means those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity.*

This was interpreted by NMFS in the EFH Proposed Rule 50 CFR Part 600 published in the Federal Register: April 23, 1997 (Volume 62, Number 78)] [Page 19726]

Sec. 600.10 Definitions.

"For the purpose of interpreting the definition of essential fish habitat: Waters include aquatic areas and their associated physical, chemical, and biological properties that are used by fish and may include aquatic areas historically used by fish where appropriate; substrate includes sediment, hard bottom, structures underlying the waters, and associated biological communities; necessary means the habitat required to support a sustainable fishery and the managed species' contribution to a healthy ecosystem; and "spawning, breeding, feeding, or growth to maturity" covers a species " full life cycle."

Furthermore, it was stated in the **Background** section of this Proposed Rule (page 19724) that:

"These proposed regulations would establish a process for Councils to identify and describe EFH, including adverse impacts to that habitat, per the requirements of the Magnuson-Stevens Act." In addition, *"Councils must submit FMP amendments containing these new provisions by October 11, 1998".*

- ***Overfished species***

The SFA defines overfished as follows:

104-297

(29) The terms "overfishing" and “overfished" mean a rate or level of fishing mortality that jeopardizes the capacity of a fishery to produce the maximum

sustainable yield on a continuing basis.

SEC. 301 of the SFA **requires** that measures must be taken to prevent overfishing as follows:

98-623

(1) Conservation and management measures shall prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery for the United States fishing industry.

SEC. 303 of the SFA further stipulates the following:

95-354, 99-659, 101-627, 104-297

(a) REQUIRED PROVISIONS. *--Any fishery management plan which is prepared by any Council, or by the Secretary, with respect to any fishery, shall--*

(1) contain the conservation and management measures, applicable to foreign fishing and fishing by vessels of the United States, which are--

(A) necessary and appropriate for the conservation and management of the fishery to prevent overfishing and rebuild overfished stocks, and to protect, restore, and promote the long-term health and stability of the fishery;

(10) specify objective and measurable criteria for identifying when the fishery to which the plan applies is overfished (with an analysis of how the criteria were determined and the relationship of the criteria to the reproductive potential of stocks of fish in that fishery) and, in the case of a fishery which the Council or the Secretary has determined is approaching an overfished condition or is overfished, contain conservation and management measures to prevent overfishing or end overfishing and rebuild the fishery;

The NMFS "Report to Congress on the Status of Fisheries of the United States" (1997) listed the American lobster along with 86 other overfished species.

Overfishing of lobster was addressed in the Strategic Assessment Workshop (SAW 22 - 1996). In this report it was stated that "the American lobster resource is considered recruitment overfished when, throughout its range, the fishing mortality rate (F), given the regulations in place at that time under the suite of regional management measures, results in a reduction in estimated egg production per recruit to 10% or less of a non-fished population." The level of fishing mortality resulting in egg production per recruit of 10% of the maximum ranged from 32% to 44% depending on the area. Currently egg production is estimated by the ASMFC at 1.5-3% and fishing mortality since 1982 has exceeded 50% every year except 1993.

In December 1997, NMFS issued the <u>EFH Interim Final Rule</u> (Federal Register: December 19, 1997 Volume 62, Number 244) Rules and Regulations [Page 66531-66559] which amended the EFH Proposed Rule as follows:

§ 600.810

Definitions and word usage.
(a) Definitions.

In addition to the definitions in the Magnuson-Stevens Act and § 600.10, the terms in this subpart have the following meanings:
Overfished means any stock or stock complex, the status of which is reported as overfished by the Secretary pursuant to § 304(e)(1) of the Magnuson-Stevens Act.

The criteria was defined in a later section of the EFH Interim Final Rule

600.815(a)(ii)(B)

If a species is overfished, and habitat loss or degradation may be contributing to the species being identified as overfished, all habitats currently used by the species should be considered essential in addition to certain historic habitats that are necessary to support rebuilding the fishery and for which restoration is technologically and economically feasible. Once the fishery is no longer considered overfished, the EFH identification should be reviewed, and the FMP amended, if appropriate.

- ***HABITAT AREAS OF PARTICULAR CONCERN (HAPC)***

The EFH Proposed Rule issued April 23, 1997 (see above) refers to these habitats as follows:

600.810 (a)(7)

Identification of vulnerable habitat. FMPs should identify vulnerable EFH. In determining whether a type of EFH is vulnerable, Councils should consider:
(i) The extent to which the habitat is sensitive to human-induced environmental degradation.
(ii) Whether, and to what extent, development activities are, or will be, stressing the habitat type.
(iii) The rarity of the habitat type.

In the EFH Interim Final Rule for Dec. 1997 (see above) NMFS responded to public comments in the following manner:

24. Comments on Vulnerable Habitats (Habitat Areas of Particular Concern)
Response:

"After consideration of comments on the proposed rule, NMFS has refined this concept to include ecological function of the habitat along with considerations of vulnerability. In the rule, NMFS renamed vulnerable habitats as "habitat areas of particular concern" (HAPC). In determining HAPCs, Councils should consider ecological value of a type or area of EFH, its susceptibility to perturbation from both anthropogenic (human-caused) sources and natural stresses, and whether it is currently stressed or rare.

Habitat areas of particular concern means those areas of EFH identified pursuant to § **600.815(a)(9**) amended as follows:

Changes

In § 600.815, paragraph (a)(9) has been renumbered from paragraph (a)(7) of the proposed rule and retitled "Identification of habitat areas of particular concern;" language has been included to denote that HAPC might include not only those areas especially vulnerable to degradation, but those that provide important ecological functions for one or more managed species; the paragraphs have been renumbered after the inclusion of paragraph (i), The importance of the ecological function provided by the habitat.

***600.815(a)(9**) Identification of habitat areas of particular concern. FMPs should identify habitat areas of particular concern within EFH. In determining whether a type, or area of EFH is a habitat area of particular concern, one or more of the following criteria must be met:*

i. The importance of the ecological function provided by the habitat.

ii. The extent to which the habitat is sensitive to human-induced environmental degradation.

iii. Whether, and to what extent, development activities are, or will be, stressing the habitat type.

iv. The rarity of the habitat type.

The following is the NEFMC Interpretation of the EFH Interim Final Rule Provisions provided by the Habitat Committee EFH Technical Team:

600.815(a)(6)(ii) For the purposes of the EFH amendment, "particularly vulnerable" means those habitat types that are most susceptible to long-lasting damage, accounting for the types of gear used in the area and the physical and biological characteristics of the habitat.

600.815 (a)(9)(i) The Technical Team will use its professional judgment as to any limiting factors or ecological "bottlenecks" that can be linked to the availability of suitable habitat. If any specific habitat areas or types can be linked in this way, these may be designated as habitat areas of particular concern.

600.815 (a)(9)(ii) and (iii) Without specific knowledge regarding the ecological function of a particular habitat area (i.e., if only Level 1 or Level 2 data are available), it may be appropriate to designate specific areas sensitive to human-induced environmental degradation or stresses from development activities as habitat areas of particular concern. The Technical Team will make this determination on a case-by-case basis.

600.815 (a)(9)(iv) The Technical Team will use its professional judgment as to the rarity of the habitat type in question and its role in supporting the managed species to determine if an area should be designated as a habitat *area of particular concern. If there is little information regarding the function of the habitat type, and this habitat type is rare, then the Technical Team will act conservatively and propose this as a habitat area of particular concern.*

The geographic range of the recommended habitat area of particular concern is limited by the extent of the scientific studies, but this should not preclude the future extrapolation of this type of designation to other areas with very similar characteristics. Although most scientific studies of the type described in the HAPC recommendation are by necessity limited in temporal and spatial scale, the conclusions and results are quite often transferable to other areas. This sort of extrapolation will depend, in large part, upon the professional judgment of the EFH Technical Team and the Habitat Advisors.

The NEFMC Technical Team for EFH has begun to apply these definitions and has recommended that a portion of Area Closure 2 be permanently closed to all fishing activities (including lobster pots) for juvenile Atlantic cod.

At the Habitat Committee Meeting on June 4, 1998, the Technical Team recommended that a second portion of Area Closure 2 and a portion of Area Closure 1 be closed to all fishing activities (including lobster pots) due to the presence of "cobble" substrate. They stated that the Western Gulf of Maine closure would be the next to be examined.

5). LOBSTER PHYSICAL REQUIREMENTS

Based on a review of the scientific literature, most of the research involving lobsters in the last century has focused on mortality tests. From these tests have come a detailed understanding of the physical and environmental conditions a lobster can endure before it dies (Fig. 3A and B). Hundreds, if not thousands, of lobsters have been killed over the years in every conceivable combination of fatal experimental conditions. From these tests, it is now clear that many of these variables work in unison and are determined to a large extent on pre-conditioning or acclimation (see Cooper and Uzmann 1980 and Jury et al. 1994).

- ***Temperature***

Without a doubt, temperature is the factor which exerts the most control on all other responses. "Temperature is the major factor controlling size at maturity, egg maturation, incidence, timing and synchronization of spawning, success of [egg] attachment and incubation and time of hatching" (Crossin et al. 1998).

The survivable temperature range in the laboratory for the American lobster is quite broad, ranging from -1^0 to 30.5^{0}C (30.2^0 to 86.9 ^{0}F.). They can also survive abrupt temperature increases of 16^{0}C (roughly 29^{0}F) or decreases of 20^{0}C or about 36^{0}F (Lawton and Lavalli 1995).

As a practical matter, lobsters normally inhabit waters where temperatures are as low as 5^{0}C (41^{0}F) or as high as 20^{0}C (68^{0}F). When the water temperature drops to approximately 5^{0}C (41^{0}F) adult molting is blocked (Waddy et al. 1995). In addition, temperatures must decline to 8^0-10^{0}C (46^0-50 ^{0}F) during winter to maintain a balance between the synchronization of the molt and ovarian cycles of the female lobster (Aiken and Waddy. 1986).

Lobster larvae have a much lower tolerance for temperatures than adults. The postlarval stage is attained at temperatures below 10^{0}C (50^{0}F), but molting to Stage V rarely occurs and survival is quite low (Ennis 1995). Temperature at hatching is even more restricted. Over a 5-year period ending in 1979, bottom water temperatures at hatching were as low as 8^0-9^0 C (46^0-48^{0}F) in samples collected in Northern New England. Temperatures ranged from 11^0-13.6^{0}C (51.8^0-56.5^0 F) in Buzzards Bay and Block Island Sound where larvae were more abundant (Fogarty 1983).

- ***Salinity***

The lower lethal limit of adult lobsters exposed to various dilution's of seawater is between 8-14 ppt (parts per thousand) depending on temperature, oxygen and acclimation conditions (McLeese 1956). Salinity's below 10 ppt cause significant physiological changes that are extremely stressful even if the animals manage to survive short-term exposure. Heavy mortality has been reported after extreme spring runoffs in estuarine systems (Thomas and White 1969). Males seem to be able to tolerate lower estuarine salinity better than females. It also appears that for larvae, "high temperature reduces tolerance to high salinity, but increases tolerance to low salinity over the 15- to 35-ppt range" (Ennis 1995).

Larvae and molting individuals are more sensitive to reduced salinity (Charmantier et al. 1988). Larval lobsters are sensitive to salinity's below 20 ppt, but these seem to be harmful only after exposure exceeding >20 days (Templeman 1936). "Tolerance to low salinity's decreases during larval development" (Ennis 1995). At a salinity of 11.6 ppt, very few Stage I larvae survive longer than 24 hours and none molt. No stage III or IV larvae survived salinity's below 12.5 ppt. No larval molting occurred beyond a salinity of approx. 40 ppt (Ennis 1995).

➢ *Oxygen*

Lobsters can survive in waters with low levels of dissolved oxygen (hypoxia), with the possible exception of locations experiencing severe organic enrichment. The lower lethal oxygen level for juveniles and adults ranges from 0.2 mg O_2/liter at 5^0C (41^0F) to 1.2 mg O_2/liter at 25^0C (77^0F) in 30 ppt salinity (Cooper and Uzmann 1980). Oxygen requirements are highly sensitive to low salinity and the American lobster consumes more than twice as much oxygen at 10 ppt than it does at 20 ppt (Jury et al. 1994a).

Larval lobsters appear twice as sensitive as juveniles and adults to reduced levels of dissolved oxygen. For larvae, "dissolved oxygen concentrations <1.0 mg O_2/liter … and pH levels <5.0 and >9.0 are lethal" (Ennis 1995).

➢ *Shelter*

Webster's New World dictionary defines shelter as "something that protects, as from the elements, danger, etc." For the lobster, shelter takes two forms: natural, "ready-made" shelters and those that must be constructed or burrowed.

Clawed lobsters "create remarkably similar burrows with one, two or more openings … The burrows begin as U-shaped tunnels (Fig. 4A) and may be expanded later into additional openings. The 'entrance' tunnel is usually a crater like, or wide-mouthed, depression with a mound of sediment at one end. The 'rear exit' and additional openings simply open onto the flat surface of the sediment" (Lawton and Lavalli 1995).

Burrowing "behavior is similar for the American and European lobsters" (Fig. 4B). A wall of excavated bottom material is generally in front of the entrance, being most conspicuous in front of recently excavated burrows. Movements into and out of the shelter tend to level off the mound. Where bottom configuration is not limiting, the walls of the burrow are generally semicircular in shape. The lobster typically rests against the inner wall with its antennae directed toward the entrance. The height of the burrow entrance is usually less than the width and the inner portion is enlarged into a chamber" (Cooper and Uzmann 1980).

"Ventilation is necessary to prevent low oxygen and high carbon dioxide stress during burrow occupancy … The construction of lobster burrows and their openings probably promotes passive ventilation. Fluid will move through the burrow from the end where the flow is slower (smaller, blunter, or lower opening) to the end where the flow is faster (larger, sharper or higher opening) … For lobster burrows in rock substrates, currents will cause water to flow between the interstitial spaces [between the rocks or gravel] thereby providing the necessary ventilation" (Lawton and Lavalli 1995).

The relationship between shelter size, substrate and lobster size (Fig. 4C) has been investigated by Wahle and Steneck (1991, 1992). Their findings "suggest that body size-substratum scaling considerations are important in habitat selection." Studies by Lavalli and Barshaw in 1986 (see also Barshaw and Lavalli 1988) indicate that small lobsters may be attacked before they even have time to construct a burrow and they remain vulnerable to excavating predators like crabs even inside the burrow. Wahle and Steneck (1991) conclude that "the American lobster appears to be restricted to shelter-providing habitats in its early benthic life, but this restriction apparently relaxes as it grows." Furthermore, Steneck (personal comm.) has shown that adult lobsters remain vulnerable to fish when tethered in deep water (i.e. Cashes Ledge). So shelter availability continues to be an important consideration.

- ***DIET***

A reduction of the food supply to larvae results in reduced survival and increased development time (Ennis 1995). However, postlarval lobsters are more resistant to starvation and survive at least 12 days of food deprivation (Ennis 1995). In fact, "the better nutritional condition and the higher growth rate of postlarvae are probably due to a higher quality of prey in the field and indicate that starvation or poor nutrition is unlikely to be a major source of natural mortality" (Juinio and Cobb 1994).

The natural diet of larval and postlarval lobsters includes the wide variety of phytoplankton and zooplankton available to them. They are generally considered to be opportunistic feeders, although they show a strong preference for live prey with a bias towards copepods and diatoms. (Fig. 5). Unlike the earlier larval stages, the Stage IV postlarva "shows increased dependence on protein and accumulates lipid stores. This probably confers considerable advantage in adapting to a benthic habitat by enabling newly settled lobsters to rely temporarily on stored reserves as they make the transition from planktonic to benthic existence" (Ennis 1995).

Plankton provides 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 the habitat differences, diet is fairly consistent for emergent and vagile phase juveniles and is dominated by mussels, lobsters, Atlantic rock crabs and gastropods (Weiss 1970).

Stomach contents of juvenile, adolescent and adult American lobsters suggest that while they consume the same type of prey, the relative proportion of the prey items taken is dependent on the size of the lobster. Smaller lobsters consume more hydroids, gastropods, crustaceans, polychaetes and brittle stars than do larger lobsters. Plants may be actively selected, forming a functional nutritional component of the diet (Weiss 1970, Hudon 1987).

"The principle components of the diet of adult lobsters are various crustaceans and mollusks, with polychaetes and echinoderms increasing in relative importance in certain areas or times of the year … there is a rapid increase to 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). Feeding slows as the result of molting in males and greater demands on females for reproduction and molting.

"With the widespread introduction of escape vents on lobster traps, it is now likely that most lobsters feed from traps before they are finally captured by the commercial fishery. In areas of intense fishing pressure, fishing bait may provide a significant [energy] subsidy, supplementing the natural food resources available on lobster grounds" (Lawton and Lavalli 1995)

6). LOBSTER PREFERENCES

It is only within the last two decades that investigators have focused on lobster habitat preferences when given a choice between two or more similar and tolerable environments. This data combined with intensive biological research on energy requirements strongly suggests that lobster preferences are linked to optimum energy efficiency throughout the lobster's life cycle. This finding is of critical importance when considering lobster habitats because it means that given a choice, a lobster will almost always select a habitat which maximizes survivability, growth, and reproductive capability (see Crossin et al. 1998 and Jury et al. 1994a,b).

There is now a general consensus that the thermal preferences of lobsters represent the temperatures at which their metabolism is most efficient (As cited in Crossin et al. 1998 pg. 371). It has been shown that lobsters are capable of detecting changes in temperatures of less than 2^0C or about 3.6^0F. They also showed that lobsters acclimated to summer temperatures (15.5 ^{0}C or approx. 60^0F) "preferred a thermal niche [or range] of 16.5^0C (61.7^0F) and avoided water that was warmer than 19^0C (66^0F) or colder than 13^0C (about 55^0F)" (Crossin et al. 1998).

This temperature preference is not surprising since the "maximum growth of juveniles and adults occurs between 15^0 and 20^0C (59^0-68^0F) [in this range]… locomotion is independent of temperature … When standardized for acclimation temperature, lobsters preferred water 1.2 ^{0} (about 2^0F) above their previous ambient temperature" (Crossin et al. 1998). In addition, most (62.5 %) summer acclimated lobsters left their shelters when water temperature was raised 8^0C (about 14^0F) to 23.5^0C (74.3^0F). When this experiment was repeated with lobsters acclimated to winter temperatures (4.3^0C or 39.7^0F) few left their shelters. In fact, 90% of the winter acclimated lobsters preferred heated shelters which were 5^0C (about 9^0F) above ambient temperature. Lobsters in the experiment seemed to avoid areas of the tank they perceived as too warm or too cold. Furthermore, "when a thermal gradient was established [on the bottom of the tank] the range of areas sampled narrowed considerably, and less overall exploration of the tank occurred" (Crossin et al. 1998).

Crossin and others speculated that lobsters which remain in certain habitats (e.g. estuaries) might eventually shift their temperature preference. They cite a laboratory experiment in which some lobsters after 12 days had very high thermal preferences between 26^0 and 29^0C (79^0-84^0F).

Among lobster larvae, temperature has little effect on survival within the range of 12^0-18^0C (54^0-64^0F) (Lawton and Lavalli 1995). This is generally consistent with the temperature range for peak occurrences (Fogarty 1983). Bottom water temperatures at peak larval densities were 8.5^0-16.0^0C (47.3 to about 61^0F) in samples collected in northern New England and 12.8^0-17^0C (55^0 to about 63^0F) in southern areas.

Lobsters are highly sensitive to changes in salinity (see Jury et al. 1994a,b). Lobsters appear to be able to sense decreased salinity of 2 ppt (from 30 to 28 ppt). When given a choice between moving through high salinity (20-25 ppt) or low salinity (10-15 ppt) passageways, nearly 93 % of the time the lobsters chose the high salinity route. In avoidance experiments at ambient temperature of 12^0-15^0C (54^0-59^0F), some animals were remarkably hesitant to move out of their shelters even when the salinity temporarily reached toxic levels below 14 ppt (Scarratt and Raine 1967, McLeese 1956). On average though, lobsters began moving when salinity's reached a level of 18.4 ppt and definitely moved away from their shelters when levels approached 12.6 ppt. (Jury et al. 1994b).

7). LIFE CYCLE

The following section is largely condensed from the remarkably comprehensive "Biology of the Lobster" (J.R. Factor, editor 1995), which offers a thorough review of previous lobster research. Every effort has been made to update the conclusions and to add new perspectives whenever subsequent research findings warranted changes. The life cycle is depicted in Fig. 6 and 7 and a brief review follows below.

- ***MATING***

Mating is a complex ritual that is intimately tied to social interactions with the dominant male and to the desirability of his shelter (see Atema and Voigt 1995, Lawton and Lavalli 1995). In naturalistic settings, only the dominant male mates with the available premolt females (Cowan and Atema 1990). To initiate courtship, males must establish a shelter large enough for two lobsters. Next, they must advertise their presence, dominance and, when possible, proven mating success to females. Since a good shelter is essential for mating success, they must demonstrate their dominance over both males and females. To dominate the most desirable large females, the male must be larger or at least of comparable size (Cowan and Atema 1990).

The "female lobsters choose the dominant male and initiate cohabitation in his shelter" (Atema and Voigt 1995). Chemical cues just prior to molting and mating appear to facilitate entering the male shelter by lowering male aggression. Field and laboratory work describe females approaching sheltered males many times before entering. Not all females can enter, however, and the sheltered males react to entering females in many ways from acceptance to vigorous rejection (Cowan and Atema 1990; as cited in Bushman and Atema 1997).

"In a naturalistic environment with two males and five females, the dominant male accepts only premolt females and cohabits with them each for a few days to weeks with a mean duration of 12 days in naturalistic aquaria … The female molts sometime during cohabitation and mating follows after 30 minutes. He climbs on her back … and begins to turn her over … The male then inserts his gonopods … into the female seminal receptacle and deposits his spermatophore with a few thrusting movements. Actual copulation lasts only a few seconds, after which the female rights herself with a tail flip out from under the male" (Atema and Voigt 1995). The male then eats most of the female's molt shell. "Females begin to show resistance to courtship after 12 hours … The 1-2 week cohabitation period is sufficient for the vulnerable postmolt female to harden her shell and still allow the male sequential access to other females" (Cowan and Atema 1990).

Although intermolt mating has been observed, it occurs mostly in prespawning, non-inseminated females or in females that have depleted their spermatophore (Waddy and Aiken 1990). The function of intermolt mating may be to allow females to replenish sperm they either failed to receive in the postmolt period or lost as a result of previous fertilization and spawning. Once inseminated, female receptivity ceases and males are usually no longer attracted (Atema and Voigt 1995).

➢ *SPAWNING*

Spawning is independent of insemination. Spawning is the passage of the egg from the ovary to the exterior of the female. Females position themselves on their back during spawning and the abdomen is flexed forward to form a brood chamber that catches the eggs as they are externally fertilized (Talbot and Helluy 1995, Templeman 1937).

Females which molt and mate in the summer usually spawn in the fall. However, if they molt and mate in the fall, then they may not mate until the following summer (Waddy and Aiken 1995). Large females have been shown to molt, then undergo two successive spawns before molting again (Talbot and Helluy 1995).

Spawning usually occurs earlier in warmer waters and depending on environmental conditions egg production can range from a few hundred to more than 100,000 eggs. Fecundity (# of eggs) is also related to the size of the female and older females generally can maintain larger broods. Spermatophores may be stored for as long as two years and normally only a fraction of the total stored sperm is used in a single spawning. More than one male may mate with a single female and sperm from both males may be used to fertilize eggs in the subsequent spawning. Eggs are attached to the mother and to other eggs by means of stalks formed from the egg coat, which are extremely durable. Nevertheless, mature "females normally lose 30-50% of a clutch during the long brooding interval of 9-16 months" (Talbot and Helluy 1995).

➢ *BERRIED FEMALES and HATCHING*

"Hatching and larval release occur following a 9- to 12-month period of embryonic development" (Ennis 1995). In order to decrease this egg development time, females have been known to migrate into warmer waters. In Canada, ovigerous females released in shallow water (Campbell 1990) migrated into "deeper water (>200 m [or about 650 ft]) exposing the developing eggs to the maximum temperature available during the winter months. Females return to shallow water the following summer to hatch their eggs when the surface temperature is high" (Ennis 1995).

Ovigerous females sometimes aggregate in certain shallows of Grand Manan at the time of hatching (Campbell, 1990). However, "the presence of stage I larvae in surface waters indicates that hatching occurs over a broad expanse in offshore waters" (Ennis 1995, see Katz 1994). "In these deep water lobsters there is no evidence of a migration of ovigerous females to coastal waters comparable to that near Grand Manan" (Ennis 1995).

Hatching generally takes place during a 4 month period from late May through much of September. The hatching season tends to begin earlier and continue somewhat longer in the southern part of the lobster's range. During hatching, 1-2000 larvae may be released at any one time and the time required to hatch and release a full clutch of eggs can vary from 15-31 days (Ennis 1995).

➢ *LARVAE*

"The 6-8 weeks of planktonic existence is arguably the most complex and least understood phase of the complex life cycle of *Homarus americanus*. This planktonic phase includes three larval stages plus a postlarval stage, during which the critical transition from pelagic to benthic lifestyle occurs" (Ennis 1995).

"The first-stage larva emerges from the prelarval molt either in conjunction with rupture of the egg membranes or up to 24 hours later, and remains attached to the cuticle" [female] (Ennis 1995). Release of free-swimming Stage I larvae is accomplished in less than one minute and occurs generally after darkness. "Immediately upon release, larvae swim upward and swarm within a few centimeters (about 1-2 in) of the surface" (Ennis 1995). Their bluish transparency matches their pelagic environment and may help to shield them from predators.

Stage I larvae are about 8 mm (0.3 in) long (Ennis 1995) and possess limited swimming ability. Depending on temperature, Stage I duration can vary from 2 days (22^0C or 72^0F) to 14 days (10^0C or 50^0F). "Stage II larvae are only slightly larger, approximately 9 mm long [or 0.35 in], and closely resemble those of the first stage" (Ennis 1995). This stage ranges from 4 to 15 days. Stage III larvae are similar but they are approx. 11 mm (0.4 in) long and they have completed a tail fan. Stage III lasts from 5 to 25 days (Ennis 1995). Curiously, larvae captured in the wild almost invariably have a shorter duration for each molt stage compared with laboratory reared larvae (Fig. 8).

All three stages possess very little horizontal swimming ability but can maintain depth control. "In coastal waters, the vertical distribution and movements of lobster larvae and postlarvae are confined to the upper 2-3 m [less than 10 feet] of the water column, whereas in offshore waters they appear to be unrestricted by depth within the upper 30 m [less than 100 ft]" (Ennis 1995).

"The wet weight of larvae increases 70-80% at each molt, but remains relatively stable between molts" (Ennis 1995). Wild caught Stage III larvae are generally larger by up to 0.5 mm (Ennis 1995). In the laboratory, "temperature has little effect on stage-specific survival of lobsters in Stages I and II (> 60 %), but survival rates in Stage III and the postlarval stage are reduced to <26% at 10^0C [50^0F], compared with those reared at higher temperatures … In the wild, the highest survival rate is associated with hatching earlier in the season, when surface temperature is increasing rapidly. This results in the most rapid growth overall and the shortest duration of planktonic life" (Ennis 1995).

➢ ***POST-LARVAE*** (4-5 mm or 0.16-0.20 in CL)

Stage IV is a postlarval stage when the animal is first recognizable as a lobster. The time it takes from hatching to attain postlarval stage varies with temperature from 11 days at 22^0C (72^0F) to as many as 54 days at 10^0C (50^0F) (Ennis 1995). At these temperatures the duration of the postlarval stage can range from 11 days to 49 days (Ennis 1995). "The postlarval lobster resembles a miniature adult, although the proportions differ, and it is now ready to make the transition from a pelagic to a benthic lifestyle" (Ennis 1995). It is brown pigmented which helps to camouflage it in the benthic substrate (see Atema and Voigt 1995).

Postlarvae possess well-balanced, stable equilibrium and they "swim with much greater agility, precision, and speed than do the earlier stages … Diving and bottom-testing behavior begin 2-6 days after molting to the postlarval stage" (Ennis 1995).

The postlarvae show a strong preference for substrate with preformed crevices and macroalgal cover (Ennis 1995). Settlement can be delayed quite considerably when unsuitable substrate is provided and molting to the first juvenile stage may also be delayed (Botero and Atema 1982). As postlarvae age or when their water has been preconditioned by fish predators they tend to settle more quickly and choose shelters less selectively (Boudreau et al. 1993). In the presence of a thermocline or thermal gradient, settlement will also be delayed and even settled postlarvae will respond to a reduction in temperature by leaving the bottom. "Remaining above the thermocline could reduce considerably the energy costs associated with the settlement process. It should be possible to determine the most likely zones of lobster settlement by mapping the thermal structure of the water column" (Boudreau et al. 1992). In general, "postlarvae are very well adapted behaviorally for locating bottom that is suitable for settling in terms of enhancing the survival of the early benthic stages" (Ennis 1995, see Cobb and Gulbranson 1983).

- ***JUVENILES***

The juvenile life history stage has been subdivided into three phases as follows (Lawton and Lavalli 1995):

> *Shelter-restricted juvenile phase* - (4 to 14 mm or 0.16 to 0.55 in CL) lobsters that have recently settled to the bottom. They retain the capacity for suspension feeding and rapid, highly effective tail-flipping.
>
> *Emergent juvenile phase* - (15 to 25 mm or about 0.6 to 1.0 in CL) exhibit a bottom foraging mode, yet only limited movement outside of the shelter. Further growth and differentiation of the claws.
>
> *Vagile juvenile* - (25 to ~40 mm or about 1.0 to 1.5 in CL) a progressive change from movements restricted to the immediate vicinity of shelter to a wider ranging surface active foraging mode and the potential for habitat shifts.

- ***ADOLESCENTS*** (~40 to 50 mm or about 1.5 to 2.0 in CL)

The adolescent phase is marked by physiological but not functional maturity. Social interactions begin to dominate seasonal movements and lobster population distribution. Onset of clear, size-related sexual differentiation. Males may become physiologically mature at a smaller size than females.

- ***ADULT*** (larger than 50 mm or about 2.0 in CL, but much larger in some areas)

The adult phase is characterized by the onset of functional maturity. Except during courtship or severe environmental stress most "adult lobsters live alone in close fitting-shelters where they spend most of their time" (Atema and Voigt 1995).

"In shallow water, lobsters generally emerge from their shelters about 1 hour after sunset and show greatest activity in the following two hours, after which they gradually return to their own shelter or a nearby alternate shelter. Some animals are resident in one shelter for up to 9 months including over wintering, others move among different shelters in a general area, and yet others are transient … Lobsters seem to 'know' their physical environment. It has been suggested that they use their activity period primarily to forage for information, not food: to update their knowledge of the physical (and social) environment" (Atema and Voigt 1995).

"In the 2 months preceding the vulnerable molt period, lobsters gradually increase the number of shelters regularly occupied to 1.9 during the last 2-week period preceding molting … Increased shelter use corresponds with increased premolt activity … Lobsters engage in extensive housekeeping, cleaning debris and silt out, pushing sand and rock and modifying the entrances. They may block entrances for up to 2 weeks with rocks or other objects … Despite these preparatory efforts … other lobsters often break though the barricades and evict the newly molted animals … Lobsters may buy time by molting in early morning, when other lobsters do not move about, thus avoiding eviction until the next night" (Atema and Voigt 1995).

Most inshore lobsters appear to be relatively local in their distribution moving less than 25 km (about 15 miles) seasonally (Lawton and Lavalli 1995). "In the Gulf of Maine, lobsters engage in small scale movements from shallow water into deeper water, apparently in response to strong winds and turbulence rather than the seasonal thermal regime" (Lawton and Lavalli 1995). Adult inshore females seem to move to deeper water earlier in the fall than adult males. "In Connecticut, long-term tag-release studies suggest that only a small percentage of the inshore lobsters migrate to deeper waters or offshore canyons" (Lawton and Lavalli 1995). Of the 21,136 tagged lobsters recaptured only 24 were found off the continental shelf. "Thus, migratory behavior of inshore lobsters in southern New England may be less common than was previously thought." (Lawton and Lavalli 1995)

"Probably 20% and possibly 30-40% of offshore lobsters annually migrate into shallow water in directed shoal ward movements the spring and summer off southern New England … Lobsters from offshore portions of the Scotian shelf and eastern Gulf of Maine undertake seasonal movements to shoal areas on Georges and Browns banks (Fig. 9). These movements from deep to shallow water may act to maintain lobsters within a temperature range of 8^0-14^0C [46^0-57^0F], allowing for more rapid growth than would be possible for lobsters either remaining inshore, where temperatures drop below 0^0C [32^0F] in winter, or remaining in deep offshore habitats, where temperatures rarely rise above 12^0C [54^0F] (Cooper and Uzmann 1971, Uzmann et al. 1977).

8).GULF OF MAINE WATER MASSES

The Gulf of Maine is a semi-enclosed coastal sea bounded by New England on the west and north, by New Brunswick and Nova Scotia on the east and north, and by Georges Bank at the shelf break. The complex current patterns in the Gulf of Maine (Fig. 10) have long interested researchers. In the 1920's, Bigelow (1927) attempted to understand these current gyres through the extensive use of drift bottles. Scientists today, even with all of their high technology instruments, are still amazed at the accuracy of his early observations (see Wiggin and Mooers 1992).

Recent temperature and salinity data are mainly in the form of profiles (Fig. 11). These have the advantage of revealing separate water masses by their temperature and salinity characteristics. Shown here is a section from the Maine coast (on the left) to Georges Bank (on the right) which clearly outlines a mass of cold intermediate water which develops in the spring and summer. This water mass sets up a pronounced thermocline (sudden temperature drop) which would be unlikely to be crossed by lobster postlarvae (see Boudreau et al. 1992).

- ***Ocean Surface Features***

<u>Temperature</u>

Although physical oceanography has traditionally depended upon relatively few temperature measurements over a brief period from research vessels, this situation is rapidly changing with the addition of satellite data. Over the last two decades, satellite remote sensing has proven to be a method by which large ocean areas could be sampled almost simultaneously at least every few days.

Satellite-derived Sea Surface Temperature (SST) data has recently been used to trace the path of warm Gulf Stream warm core rings (WCR) as they invade the southern flank of the Georges Bank (Fig. 12). The area shown in red (Fig. 13) is as much as 8^0C (approx. 14^0F) warmer than the surrounding waters (Conkling 1995).

<u>Current Patterns</u>

Part of the oil companies' plans for drilling on the Georges Bank involved an analysis of Gulf of Maine current patterns on a monthly basis. These maps (Fig. 14 A-L), which are unfortunately out of print, were part of the Environmental Impact Statement for Lease Sale 42. They reveal the complex interaction of coastal winds and Gulf Stream waters. The counterclockwise current pattern appears to be most pronounced during the spring and then weakens towards late summer. Recently updated maps based on the latest technology have been modeled at the University of Maine.

Salinity's

Little has been published on the overall salinity regime of the Gulf of Maine. Perhaps one of the best maps (Fig. 15) is by Brooks showing data for June 1983 (see Wiggin and Mooers 1992). His map shows the influence of fresher cooler waters extending down the coast and across the northern flank of Georges Bank. Details of Georges Bank salinity at a depth of 20 m or about 66 ft (Fig. 16 A and 16B) reveal a tongue of fresher water crossing the central bank during the winter. Note the rapid increase in salinity along the shelf margin during both seasons (Backus 1987).

Dissolved Oxygen

Dissolved oxygen levels on Georges Bank (Fig. 17A and 17B) vary greatly with the seasons from a high around 8.6 mL/L in winter to around 6.0 mL/L in summer. Lowest dissolved oxygen levels are found in the deep slope waters and locally could form anoxic conditions in the deeper canyons (Backus 1987).

➢ ***Bottom Temperatures***

Data on bottom temperature is sketchy and comes from a variety of sources. The only comprehensive bottom temperature map available goes back to the early 1960's (Fritz 1965). This map gives an average of bottom temperatures (Fig. 18A and 18B) over a 6-year period between the months of September to November based on 761 stations in the Gulf of Maine and adjacent waters (Fig. 19A and 19B). It showed bottom temperatures ranging from 6^0 to 7^{0}C (43^0-45^{0}F) along the coasts of Maine and Massachusetts reaching a maximum of 11^{0}C (52^{0}F) in Cape Cod Bay and 14^{0}C (57^{0}F) near Martha's Vineyard. Across Georges Bank the bottom temperature reached 15^{0}C (59^{0}F) and along the southern edge of the bank the temperature varied from 11^0-13^{0}C (52^0-55^{0}F).

Large scale, generalized, bottom temperature maps of the same area were included in a study of fish distribution in the New York Bight (Grosslein and Azarovitz 1982). These allow us to compare bottom temperatures between autumn and spring for the years 1973 and 1974 (Fig. 20A-D). Unfortunately, there is no precise information provided on the number of stations sampled or the frequency of sampling. These maps show spring temperatures as low as 4^0 to 6^{0}C (40-43^{0}F) along the coasts of Maine and Massachusetts averaging about 6^{0}C across Georges Bank. They show minimum temperatures south of Georges Bank of 8^{0}C (46^{0}F) out to the 1000 m (about 3200 ft) depth contour. In autumn, bottom temperatures rose as high as 16^{0}C (61^{0}F) on Georges Bank, but remained in the 8^0-10^{0}C (46^0-50^{0}F) range on the southern edge.

Bottom Temperature Changes

Some work has also been done (Fig. 21) on the changes and trend in bottom temperatures over an 8 year period (Davis 1978). This work indicates that during autumn the mean bottom temperature in the Gulf of Maine increased rather steadily from a low of 5.4 ^{0}C (41.7 ^{0}F) in 1966 to a high of 8.4 ^{0}C (47.1 ^{0}F) in

1974. A similar pattern was observed in the fall temperatures. Davis assumed that fluctuations in the volume of slope water entering the Northeast Channel were mainly responsible for the general temperature trend.

9). HABITAT CHARACTERISTICS

A complete inventory of all available habitats is beyond the scope of this paper. Only those environments which have been identified or suggested as potential lobster habitat are evaluated below:

- ***INSHORE LOBSTER HABITATS***

  - Estuaries

The estuaries of the Gulf of Maine are fed by a vast watershed (Fig. 22) covering 178,000 sq. km (69,000 sq. miles) which empties 950 billion liters (251 billion gallons) of freshwater into near shore environments each year. Within the US, the 17 major estuary systems comprise some of the most productive ecosystems on the planet (Platt 1998). Lobsters reportedly utilize the following habitats in these areas: (see Cooper and Uzmann 1980)

> Mud base with burrows - These occur primarily in harbors and quiet estuaries where currents are usually not a major factor. Lobster shelters are formed from excavations in soft substrate. Cooper and Uzmann (1980) reported lobster burrows at depths of 30-60 m (about 100-200 ft) in the Sheepscot Estuary. Lobsters excavate burrows 60-80 cm (about 24-32 in) below the sediment water interface at a relatively steep angle of 40-90 degrees. During the winter lobsters may take shelter in a mud burrow and close off the entrance with a partition of sediment and debris; they can remain enclosed in this shelter for weeks or months at a time. To the north, off Prince Edward Island, burrows reportedly had a diameter about the size of the lobster and were spaced about 2 m apart. (Densities up to 20 lobsters per sq. m or about 17 per sq. yd for small juveniles. Adults probably less than 0.01 lobsters per sq. m or 0.008 lobster per sq. yd) (Cooper and Uzmann 1980).
>
> Rock, cobble and gravel - Investigators at the University of New Hampshire (Brown et al. unpub.) have modeled lobster habitats in the Great Bay Estuary (Fig. 23A and 23B). They have found that in Great Bay Estuary, juvenile lobsters apparently occupy a relatively small stretch about 6.5 km (4 mi) long near the mouth of the Piscataqua river system. Furthermore, it is evident that these juvenile lobsters prefer shallow bottoms with gravel and gravely sand substrates (Fig. 24) where salinity remains high and temperature is relatively moderate throughout the year. All of these conditions occur in a contiguous area covering less than 1000 acres. Another tiny area in Great Bay Estuary may provide limited shelter for juveniles among eelgrass.
>
> In Maine, researchers at the Darling Marine Center (Steneck and Wilson 1998) have found that lobster population densities appear greater west of Penobscot Bay than they are to the east (Fig. 25). This could be due to currents, distribution of gravel/cobble substrates or a combination of these and other factors.

Near the mouth of Penobscot Bay, they have also shown a high concentration of lobsters. Settlement densities (Fig. 26) totaled more than 1 lobster per sq. meter or roughly 0.8 per sq. yd. Young lobsters (Fig. 27) were also observed at high densities (over 0.5 juvenile lobsters per sq. m or 0.4 per sq. yd and more than 0.75 adolescent lobsters per sq. m or about 0.63 per sq. yd).

In Rhode Island, one of the primary estuarine surveys was done by Wahle (1993). His study showed that "Based on direct benthic censuses along a 22 km (about 14 miles) length of Narragansett Bay Estuary, new benthic recruits were absent from featureless sedimentary habitats that form the majority of the bottom in this shallow bay (generally less than 10 m or about 30 ft deep). Rocky habitat and cobble /boulder habitat supported both new recruits and older lobsters; mechanisms for an apparent restriction of recruitment at upper-bay sites were suggested to be reduced larval supply and physiological stress" (Lawton and Lavalli 1995).

<u>Rock/shell</u>

The adult lobsters at Great Bay Estuary also utilize the sand and gravel environment in the channels, but appear to prefer a rock/shell habitat more characteristic of the high temperature, low salinity regimes of the central bay. While this habitat in Great Bay Estuary is more extensive than that occupied by juveniles, it still involves only about 5000 acres, which is about 20% of the estuary (see Fig. 23 and 24).

- Wetlands and Salt marshes

According to NMFS' Office of Habitat Conservation (personal communication), the relationships between wetlands and fish production are an essential and important part of the ongoing debate on wetland regulation and policy. Unfortunately, these relationships are complicated and often unappreciated. For a few fisheries, such as American lobster, the importance of wetlands has been discovered only recently, and the primary influences on productivity are still being investigated. Because of the complexity of aquatic systems, it is difficult to quantify the exact effect of the loss or degradation of a particular acre of wetland on the fishery as a whole.

Estuaries depend on their wetlands to maintain water quality and provide the basis for food chains that culminate in human consumption of seafood. These wetlands are the source of runoff and nutrients for many of the estuarine and coastal habitats. They influence the temperature and salinity regimes for these areas and indirectly influence the habitat selections of the American lobster.

In the late 1970's and early 1980's, this country was losing wetlands at an estimated rate of 300,000 acres per year. The Clean Water Act and state wetland protection programs have helped to decrease wetland losses to an estimated 70,000 to 90,000 acres per year.

New England is continuing to lose wetlands at an alarming rate. In Maine, the extensive coastal rivers, bays and estuaries support both recreational and commercial fisheries for finfish and shellfish. Key commercial species, such as the American lobster, depend on Maine's extensive estuarine and marine wetlands for food and protection as juveniles and adults. Maine, while not subject to the intense development pressure of its neighbors to the south, nevertheless had lost approximately 20% of its estimated original wetlands base by the mid 1980's. This compares with 9% for New Hampshire, 28% in Massachusetts, 38% in Rhode Island and 74% in Connecticut.

- Peat

Lobster shelters are formed from excavations that cut deep into peat; they are often obscured by dense algal growth. The reef forms from blocks of salt marsh peat that break and fall into adjacent marsh creeks and channels (Fig. 28). Additional research is needed to relate the satellite imagery directly to known lobster areas. However, we do know that peat reefs are often associated with marsh grass (*Spartina*) and appear to provide moderate protection for lobsters against fishes and crabs. This is presumably because lobsters blend in with root structures (Barshaw and Lavalli 1988). (Densities up to 5.7 individuals per square m or about 4.8 ind. per sq. yd.)

- Island Margins

The coast of the Gulf of Maine is over 7000 miles long and is littered with islands. It has long been recognized that the character of the coastline and associated islands is strongly influenced by the underlying geology (Fig. 29). The state of Maine alone has over 4500 separate islands which are supported mainly by granites. As the satellite photo of the central Maine coastline shows (Fig. 30), conditions exist for enhanced productivity along the island margins. Each island influences currents which help to mix, oxygenate, and enrich the water. The islands also cause local up welling of deeper, colder, nutrient rich waters. It has long been recognized that island margins can provide ideal conditions for lobsters. "It is no accident that Maine's largest lobster harvests are found along the section of coast with the largest number of islands" (Conkling 1995).

- Kelp Beds

The relationship between lobsters and kelp habitats provides important clues about how American lobsters adapt to altered habitats and their ultimate carrying capacities. In order to fully understand these associations, we must first investigate the kelp forests themselves.

Kelp beds in New England consist primarily of seaweed species of *Laminaria longicruris* and *L. saccharina* (locally referred to as kelp.). These kelps inhabit sub tidal areas from Canada to Long Island Sound (Egan and Yarish 1990). Kelps possess a fairly low maximum temperature tolerance and certain forms begin dying off at temperatures above 16^0-18^0C (61^0-64^0F). Its optimum temperature range is even more restrictive and at its southern limit, the most rapid growth period occurs during spring when water temperatures are 10^0-12^0C (50^0-54^0F) (Egan and Yarish 1990).

Kelp distribution is known for only a few isolated areas in Maine. In Penobscot Bay, kelp beds develop on some of the nutrient enriched rocky bottom habitats which are prime lobster grounds (Platt 1998). In addition, kelp forests have been mentioned as "one of the preferred habitats where lobsters hide during the period they are shedding their old shells" (Conkling 1995). Unfortunately, we did not have access to an accurate map showing the distribution of kelp beds along the entire New England coast. Therefore, it was not possible to map this habitat in relation to lobster abundance in general. Nevertheless, lobster behavior in kelp beds could tell us much about how lobsters adapt to habitat changes.

In recent years, field studies have been conducted to determine how lobsters use kelp beds as habitat (Bologna and Steneck 1993). The site chosen was the so-called "Thread of Life" located between Rutherford Island and Crow Island off the Central Maine coast. Although natural kelp beds were found throughout this region growing on scattered hard substrate in the featureless sediment, extensive kelp beds do not naturally occur here (Bologna and Steneck 1993).

Experimental kelp beds were transplanted and control plots were established on relatively featureless silty-sand substrate in sub tidal regions 10-15 m (33-49 ft) deep. Water temperatures at this location ranged from 2^0-3^0C (36^0-37^0F) in winter to 15^0-16^0C (59^0-61^0F) during the summer. They used only kelp greater than 50 cm (about 20 in) total length because "only large kelp were commonly observed sheltering lobsters … Beginning in late spring and lasting through early fall the region is commercially fished for lobsters" (Bologna and Steneck 1993).

The average size of the 1423 individual lobsters which were attracted to the kelp beds during this two year study ranged from 51-61 mm CL (approx. 2-2.5 ft CL) indicating that most of the lobster were adolescents (Bologna and Steneck 1993). While physiologically mature, these individuals were probably not functionally mature.

The results showed that "population density and biomass inside transplanted kelp beds (1.20 to 1.68 ind. per sq. m or 1.0 to 1.4 ind. per sq. yd) were significantly higher than in control regions (0.14 ind. per sq. m or about 0.12 ind. per sq. yd). Lobsters did not burrow into the sediment, but sought shelter beneath the kelp. No difference in lobster density was observed between live and artificial [plastic] kelp treatments, but both treatments maintained lobster densities and biomasses that were an order of magnitude greater than adjacent control regions" (Bologna and Steneck 1993). Perhaps of more importance is the fact that lobster density was significantly greater in the smallest patches. "Moreover, lobsters typically occupied the edges of kelp beds and their abundance within kelp patches increased" as the exposed perimeters increased (Bologna and Steneck 1993). It was theorized that "lobsters use edges of kelp beds to maximize their sensory input while still allowing them to remain under cover." This suggests that "edge effects influence the local carrying capacity for lobsters by influencing the lobster's choice of kelp beds as habitat" (Bologna and Steneck 1993). Furthermore, these edge effects appear to be limiting lobster abundance along the bed perimeter.

- Rockweed

Rockweed, *(Ascophyllum)* is a species of macroalgae common to Gulf of Maine marine and estuarine intertidal areas. Distribution is influenced by tidal elevation, salinity, wave energy, exposure to ice, and substrate (Fig. 31). While it typically adheres to rocky substrate, a form of rockweed (*Ascophyllum nodosum ecad scorpioides*) grows in salt marshes, over organic and sandy soils. The various ecological functions of the extensive rockweed beds are just beginning to be understood, and its importance to lobsters has not yet been assessed (Conkling 1995).

- Eelgrass

Eelgrass (*Zostera*) is a submergent, vascular plant typically growing in sub tidal inshore waters along the middle and northern Atlantic seaboard. It requires a muddy to sandy sediment, which is usually associated with moderate water currents and limited wave action (Fig. 32). Eelgrass beds serve as structure and cover for marine and estuarine vertebrates and invertebrates, and as a primary producer of organic matter (Conkling 1995). Lobster shelters are sometimes formed from excavations into rhizomes of eelgrass meadows like those found off Nantucket (Fig. 33). Curiously, eels are often seen occupying these lobster shelters and they might be partly responsible for decreases in lobster densities over a seasonal period.

In Great Bay Estuary, some lobsters have been associated with eelgrass beds (Brown et al. unpub.). However, it does not appear that eelgrass provides any more protection from predators than does mud substrate (Barshaw and Lavalli 1988). (Densities fewer than 0.04 ind. per sq. m or about 0.03 per sq. yd; mostly juveniles and adolescents.)

- Intertidal Zone

Recently volunteers at the Lobster Conservancy (Diane Cowan, personal comm.) have conducted a census of lobster nursery grounds along the coastline of Harpswell, Maine. This survey called the Intertidal Lobster Monitoring Program (ILMP) was conducted under a grant from the Davis Conservation Foundation. The ILMP confirmed the presence of early settlement, postlarval and juvenile lobsters in the lower intertidal zone in that area. Similar sampling efforts in New Hampshire, Massachusetts, Rhode Island, and Connecticut show that young-of-the-year and juvenile lobsters do use this habitat and that it may be more important than previously expected. This intertidal sampling effort underscores the importance of mapping the lobster nursery grounds in detail before they are altered or destroyed by human activities. (Densities up to 4.33 individuals per sq. m or about 3.25 per sq. yd; mostly juveniles and adolescents.)

- Inshore Rock Types (Fig. 34)

<u>Sand base with rock</u> - This is the most common inshore rock type where the depth is generally greater than 40 m (approx. 130 ft). It consists of sandy substrate overlain by flattened rocks, cobbles and boulders. Lobsters are associated with

abundant sponges, Jonah and rock crabs. Shelters are formed by excavating sand under a rock to form U-shaped, shallow tunnels. (Density of 3.2 lobsters/sq. m or about 2.7 per sq. yd with avg. CL = 40 mm or 1.57 in) (Cooper and Uzmann 1980).

Boulders overlying sand - This rock type is best described off McNutt Island Nova Scotia. It is relatively rare for inshore New England (Densities range from 0.13 to 0.09 ind. /sq. m or about 0.11 to 0.08 ind. per sq. yd.)

Cobbles - shelters formed in the interstitial spaces between rocks, pebbles and boulders making up the bed. (Densities up to 16 ind. per sq. m or about 13 ind. per sq. yd.)

Bedrock base with rock and boulder overlay - This rock type is relatively common inshore from low tide to 15-45 m (or about 50-150 ft). Burrowing is generally not possible on this substrate. Shelters are formed by rock overhangs or crevices. Encrusting coraline algae and attached organisms such as anemones, sponges and mollusks cover exposed surfaces. Green sea urchins and starfish are common. Cunner, tautog, sculpin, sea raven and redfish are the most abundant fish occupying the bedrock-rock habitat. (Density of 0.1 lobsters per sq. m or about 0.08 per sq. yd up to 0.3 lobsters per sq. m or 2.5 per sq. yd in summer closures).

Mud-shell/rock substrate - Best described off Rhode Island. (Density of 0.15 lobsters per sq. m or about 0.13 per sq. yd). Usually found where sediment discharge is low and shells make up the majority of the bottom.

- ***OFFSHORE LOBSTER HABITATS (Fig. 35)***

Sand base with rock - consists of sandy substrate overlain by flattened rocks, cobbles and boulders. Although common inshore, this habitat is rather restricted in the offshore region except along the north flank of Georges Bank.

Clay base with burrows and depressions - common to the outer shelf and upper slope. Burrows excavated by lobsters up to 1.5 m (nearly 5 ft) and frequently having an object in the center such as a boulder, rock or cast-off debris. Large bowl-like depressions range in size from 1.0 to 5.0 m (roughly 3-15 ft) in diameter and may shelter several lobsters at a time offshore. (Minimum density of 0.001 lobsters per sq. m in summer). (Cooper and Uzmann 1980)

Mud-clay base with anemones - common habitat for lobsters on the outer shelf or upper slope. Anemones are 20-35 cm (about 8-14 in) tall with a diameter of 5-10 cm (about 2-4 in) at their base. Forests of mud anemones may reach densities of 3 or 4 per square meter (roughly 2.5-3.3 per sq. yd). Depressions serve as shelter for relatively small lobsters. Generally within the 50-80 mm (roughly 2-3 in) CL size range. (Minimum density of 0.001 lobsters per sq. m or 0.0008 per sq. yd. in summer.) (see Cooper and Uzmann 1980).

Mud base with burrows - occurs offshore mainly in the deep basins (up to 250 m or about 820 ft). This environment is extremely common offshore. There are, as yet, no estimates available of lobster density in this setting.

Clay Pipes - characterized by hollowed out pieces of hardened sediment of irregular shapes and sizes that lie littered on the seabed in selected areas. The origin of clay pipe is uncertain. However, one possible explanation is that burrows made by worms, crabs, lobsters and other organisms have become hardened by iron rich waters percolating through the burrow walls (Valentine personal comm.). Another theory is that clay pipes are the remains of tree roots. Whatever their origin, these habitats appear to be shrinking. Anecdotal evidence suggests that clay pipe areas have been disturbed by fishing gear.

In Massachusetts, clay pipes were once a prominent feature of the sea floor on the northern edge of Stellwagen Bank. This is consistent with the large percentage of clay bottom in this region. For reasons of their own, lobstermen have been reluctant to reveal the location of historic or current clay pipe areas. As a result, it is not known whether they are found in other predominantly clay substrates.

- **Submarine Canyons**

The following summary is based heavily on the unsurpassed descriptions of the actual scientists who have participated in more than 200 dives in submersibles in the canyons off Georges Bank (Cooper et al. 1987). We have frequently quoted directly from them in order to capture the flavor of their first-hand sightings and the depth of their experience.

There are more than 15 submarine canyons that cut into the shelf edge on the south side of Georges Bank (Fig. 36). These are V-shaped, sinuous valleys which resemble canyons of fluvial (river) origin. These canyons were first surveyed in the 1930's, but they were not fully explored until manned submersibles were used extensively in the early 1980's. Since that time, one of the largest, Oceanographer Canyon, has been studied most thoroughly (Fig. 37). Fortunately, the results are generally applicable to the other major canyons.

These canyons present a diverse group of habitat types made possible by the rapid changes in substrate and the abundance of nutrients distributed by the strong currents. The canyons present habitats which are recognized as important nursery grounds for a number of bottom animals including lobster, crabs, tilefish and hakes. Juveniles of these species have been observed in naturally occurring and excavated shelters in the bottom, in both the semi-consolidated sandy silts and in the boulder fields. "Concentrations of lobsters (*adolescents* and adults), for example are substantially greater in submarine canyons than in areas nearby; lobsters seen inside the canyons are usually adolescents (<80 mm or less than about 3.15 in CL) while those nearby but outside the canyons are usually adults" (Cooper et al. 1987).

Sediments in Oceanographer Canyon and most of the other canyons are influenced by the strong clockwise currents on Georges Bank which flow westward across the shelf and by tidal currents which flow up and down the axes. As a result, the canyon sediments are strongly asymmetrical (uneven) with gravel pavements and boulders along the eastern canyon rim and with mostly sand along the western wall. On the east wall, the thin gravel pavement predominates from about 150 to 300 meters (about 500-1000 ft) and the underlying silts or muds are frequently exposed in scattered burrows. Cobbles and boulders up to 1 m. (3.3 ft) in length occur in the gravel pavement. Currents as strong as 1-2 knots distribute sand and sandy-silt along the western canyon wall and the canyon floor is covered with ripples and dunes of slightly gravely sand. These sand dunes which are 1-3 m (about 3-10 ft) in height, were only observed in Oceanographer, Hydrographer and Gilbert canyons; the other canyons south of Georges Bank had only rippled sand. From about 300 to 500 m (about 1000-1500 ft) a clay-like sandy silt or mud is riddled with burrows of lobsters, crabs, fish or anemones. These burrows are often found on steep cliff faces and occasionally these structures collapse, dropping angular slabs onto the canyon floor and leaving vertical walls 10-15 m high (about 30-50 ft).

"Faunal diversity and, to some extent, abundance in the Georges Bank canyon heads appear to be closely tied to the presence of cobbles and boulders on the ocean floor and to exposures of the consolidated sandy silt into which various animals tunnel and burrow. Commercial concentrations of lobsters occur in depths of 100-300 m (about 300-1000 ft) in and near the canyons and over the slopes between them" (Cooper et al. 1987).

The following classification of submarine canyon habitat types is modified from Cooper and Uzmann 1980 and Cooper et al. 1987. The faunal characterization is based on the shallow 150-229 m (492-751 ft) depth zone only.

Type I - Canyon rim and walls consists of sand or semi-consolidated silt substrate (clay-like consistency) with less than 5% overlay of gravel. Characterized by a burrowing mud anemone. Relatively featureless except for conical sediment mounds along canyon axis. (Densities of 0-2 lobsters per 10,000 sq. m or about 2 1/2 acres; mostly adolescents and adults.)

Type II - Canyon walls consist of gravely sand, sand or semi-consolidated silt substrate (clay-like consistency) with more than 5% overlay of gravel. Relatively featureless. Burrowing mud anemones live in tubes that project 10 cm (about 4 in) or more above the bottom and the animal itself may extend another 10-15 cm (about 4-6 in) above that. Also associated with Jonah crabs, ocean pout, starfish, rosefish, squirrel hake. (Densities up to 10 lobsters per 10,000 sq. m or about 2 1/2 acres; mostly adolescents and adults.)

Type III - Rim and Head of Canyons and at base of walls. Sand or semi-consolidated silt (clay-like consistency) overlain by siltstone outcrops and talus up to boulder size. Featured, very rough bottom with erosion by animals and scouring. Lobsters associated with, rock anemones, Jonah crabs, ocean pout, tilefish, starfish, conger eels and white hake. (Densities of 5-1260 lobsters per 10,000 sq. m or about 2 1/2 acres; mostly adolescents and adults.)

Type IV - Pueblo villages- Submarine canyon clay wall with burrows. Heads of Canyons to middle canyon walls consolidated clay substrate, heavily burrowed and excavated. Slope 5 degrees to 70 degrees but generally more than 20 degrees and less than 50 degrees. Juvenile and adult lobsters and associated fauna create borings up to 1.5 m (nearly 5 ft) in width, 1 m (about 3 ft) in height and 2 m (about 6 ft) or more in depth. Between 5 to 10% of borings have multiple openings. Lobsters associated with Jonah crabs, tilefish, shell-less hermit crab, ocean pout, starfish, and conger eels (Fig. 38). (Densities of 5-1260 lobsters per 10,000 sq. m or about 2 1/2 acres; mostly adolescents and adults.) This habitat may well contain the highest densities of lobsters found offshore.

Type V - Sand dune substrate located along the axis. It is associated with white hake, Jonah crab and goosefish. Few, if any, resident lobsters are found in this environment.

10). ROCK AND SEDIMENT DESCRIPTIONS

Before we can begin a meaningful interpretation of the habitat distribution data, we must first examine the different sediment classifications and some of the inherent problems. Much confusion has resulted from a lack of uniformity in sediment names. These are not merely fine points of semantics. Undoubtedly, it is this confused nomenclature which is partly responsible for many of the misconceptions about the relationships between lobster distribution and substrate.

The basic sediment size classification was developed by Wentworth in 1922. It was modified by the Lane committee (Lane et al. 1947). The modified standard lists 5 grades of sand from very fine to very coarse and subdivides gravels into gravels, pebbles, cobbles and boulders (Fig. 39). This is the scheme which most of the lobster researchers have followed when describing habitat.

Unfortunately, the United States Geological Survey (USGS), in order to be consistent with other federal agencies, has chosen to lump all sediment sizes larger than coarse sand into the gravel category. The state geological surveys generally follow the USGS convention. To make matters worse, the USGS has retained the unofficial designation of "bouldery seabed" to designate areas which are predominately boulders. This means that it is necessary to extrapolate (estimate) from the USGS maps the approximate location of the pebbles, cobbles and boulders.

Additional confusion is created with the rock names for sand and gravel mixtures (Fig. 40). At the USGS, a sample is considered a gravel if it contains more than 50% gravel or larger particles by weight. It is considered a sand if it contains more than 50% sand by weight and it is considered a silt or clay if it contains more than 10% by weight of either of these two components.

To clarify the terminology, the traditional standard for Sedimentary Rocks (Pettijohn 1949) provides the following basic definitions:

> *Boulder* - "a detached rock mass, somewhat rounded or otherwise modified by abrasion in transport and larger than a cobble" with a minimum size of 256 mm (about 10 in).
>
> *Block* - "a large angular fragment showing little or no modification by transporting agencies."
>
> *Cobble* - similar to a boulder, but it is restricted in size from 64 mm (~2.5 in) to 256 mm (~10 in)
>
> *Pebble* - "a rock fragment larger than a sand grain or granule and smaller than a cobble, which has been rounded by the action of water wind or glacial ice. It is therefore between 4 mm (~0.15 in) and 64 mm (~2.5 in)".
>
> *Gravel* - the unconsolidated accumulation of pebbles, cobbles and boulders. Later "gravel" replaced the abandoned term "granule" to indicate grains 2 mm (~0.07 in) to 4 mm (~0.15 in) in size.

Sand - aggregate of mineral or rock grains greater than 1/16 mm (~0.0025 in) and less than 2 mm (~0.07 in) in diameter.

Silt- less than 1/16 mm (~0.0025 in) and greater than 1/256 mm (~0.00015 in).

Mud- a somewhat informal term referring to a mixture of silt, clay, and fine sand with sand usually making up less than 20-50% of the sample depending on the amount of clay. Most marine mud's are land-derived having been transported into quiet water primarily by major rivers.

Clay - anything less than 1/256 mm (approx. 0.00015 in)

11). INTERPRETATION AND DISCUSSION

➢ Lobster Larvae Dispersal

Larval dispersal has been a subject of considerable interest over the last 20 years with many different theories proposed to explain larval densities. However, this controversy has largely been silenced by the work of Katz and others (1994) who have documented one mechanism of dispersal from the submarine canyons. They began with a linear collection of surface samples from the submarine canyons to Martha's Vineyard (Fig. 41). Significantly, the data shows a high percentage of larvae but no postlarvae (PL) in the vicinity of the canyons. The high levels of Stage I larvae near the canyons are important because, as we saw in Figure 8, the Stage I duration in the wild is less than 5 days. The researchers then modeled ocean currents, wind velocities and various swimming speeds for the different larval stages. Their results (Fig. 42) show that some of the many Stage IV postlarvae found near Martha's Vineyard could have arrived from the canyon areas within the duration of the planktonic phase. Just as important, the length of each arrow on the map indicates the distance that the larvae could travel within five days. This shows conclusively that the Stage I larvae must have been released within the distance of one arrow from where they were sampled and, given the current and wind directions, the most likely release point would be the submarine canyons.

We can now apply this same technique to the earlier work by Fogarty and others (1983). They not only showed the overall annual density of larvae along the New England coast (Fig. 43), they provided a breakdown of larval stage composition and temperature (Fig. 44). From this data we can conclude that in areas with a high percentages of Stage I larvae, the eggs must have been released by brood stock females located within a relatively short distance of the surface sampling stations. Future tight surface sampling grids have the potential to identify the probable brood stock areas throughout the Gulf of Maine.

Another dispersal method has been documented in Canada (Cobb and Wahle 1994). Larvae are more abundant near Browns Bank than inshore. Drift bottle studies suggest that all larvae produced here would be transported near shore to Nova Scotia, Bay of Fundy and along the coast of Maine.

➢ LOBSTER HABITAT UTILIZATION

A review of the available lobster habitats leads to the following conclusions about Essential Lobster Habitats:

Inshore Lobster Habitats

ESTUARIES

Mud base with burrows - A probable Essential Lobster Habitat for juveniles and possibly adults.

Rock, cobble and gravel - These habitats represent critical nursery grounds for the American lobster and should be given a high priority in designating Essential Lobster Habitat for postlarvae, juveniles, adolescents and possibly adults.

Rock/shell - Often found near the high temperature, low salinity regimes of a central bay. Since a small group of lobsters always seem to prefer relatively high temperatures and low salinity's on tests, it is unclear how significant this habitat is for adult lobsters. More work needs to be done on-site under these extreme conditions before we can determine if this is an essential habitat. It is likely that many of these adults can adapt and would simply migrate to more moderate environments were this habitat to become more stressed.

WETLANDS

The continued loss of wetlands should be of concern to lobster harvesters and lobster managers, but for the most part, wetlands do not strictly represent an Essential Lobster Habitat with one notable exception:

Peat Reefs

- All life stages have been reported with shelter-restricted and emergent juveniles most common. Apparently a very limited but important environment which would probably be considered Essential Lobster Habitat.

ISLAND MARGINS - It is likely that the island margins themselves will eventually be designated Essential Lobster Habitat for all life stages.

KELP BEDS - Not only is the study of kelp beds important in light of sea urchin destruction of kelp forests, but it may be significant with regards to "edge effects" in other habitats as well. In this case, the field studies indicate that kelp beds on sandy substrates almost certainly represent an Essential Lobster Habitat for adolescent lobsters. More research is needed to find if kelp beds are used by lobsters in relation to other substrates.

ROCKWEED - While rockweed may provide an important food supplement for small lobsters, little research has been published on their utilization as a primary habitat. It is likely that they merely add to the effective camouflage of lobsters hiding under the rocks and do not represent an Essential Lobster Habitat.

EELGRASS - The regional importance of eelgrass beds as a lobster habitat appears to be minor, but adequate studies are still lacking. Until more is known, and according to the conservative approach adopted by NMFS, they should probably be considered Essential Lobster Habitat.

INTERTIDAL ZONE - Since this habitat has only been recently identified as one that lobsters utilize, it is difficult to determine the relative importance of it as an Essential Fish Habitat. However, given the fact that shelter-restricted, emergent, and vagile juveniles have been found in this habitat in 5 New England states, NMFS should probably adopt a conservative approach here. This habitat also has one of the greatest potentials to be strongly impacted by human activities.

INSHORE ROCK TYPES

Sand base with rock - An important and probable Essential Lobster Habitat for all life stages.

Boulders overlying sand - This is generally a limited habitat inshore but may be an important or Essential Lobster Habitat for juveniles.

Cobbles - This appears to be a prime habitat for settlement and nurseries and should probably be considered Essential Lobster Habitat for post-larvae, juveniles, and some adolescents.

Bedrock base with rock and boulder overlay - An important and probable Essential Lobster Habitat for vagile juveniles, adolescents, and adults.

Mud-shell/rock substrate - This is a limited habitat but locally may be an important or Essential Lobster Habitat for juveniles.

OFFSHORE LOBSTER HABITATS

Sand base with rock - This type is not very common, but almost certainly is an Essential Lobster Habitat for all life stages.

Clay base with burrows and depressions - Apparently depth-restricted, but a probable Essential Lobster Habitat for adolescents and adults.

Mud-clay base with anemones - An extremely fragile environment which is also severely depth-restricted. It is a strong candidate for an Essential Lobster Habitat for adolescents and adults.

Mud base with burrows - Its importance as a critical lobster habitat has not yet been demonstrated.

Clay Pipes - There have been numerous anecdotal reports of clay pipes serving as lobster habitat and until more is known they should probably be considered Essential Lobster Habitat.

Submarine Canyons
The offshore submarine canyons represent a particularly important habitat for abundant adolescent and adult lobsters and should be especially protected as an Essential Lobster Habitat.

➢ Habitat Distribution and Substrate Maps

As the limited habitat definitions above show, most marine environments are strongly influenced by the character of the sea floor sediments. The substrate maps prepared for this report are a mosaic of previous maps updated and revised to show the areas which have been studied in detail. The following investigations form the framework for these maps.

The primary map used is the United States Geological Survey (USGS) Distribution of Surficial Sediment for the Gulf of Maine and Georges Bank (Poppe et al. 1989) which extends offshore from Rhode Island to Nova Scotia. Figure 45 A is a reduced version of this map. In addition, (Fig. 45B) includes a detailed portion of the original colored map centered on Cape Cod. This map was compiled from the work of John Schlee in the early 1970's and was reissued by the U.S. Minerals Management Service (MMS) for the Dept. of Interior's draft environmental impact statement (DEIS) for oil and gas leases in Sale #42. It was listed as Visual No. # 3 (Bottom Sediments) and is unfortunately out of print. These maps were based primarily on bottom grab samples at 3620 stations including about 5% of the samples which were obtained by coring. As is common in this type of investigation, bathymetric (depth) contours were used as a guide in placing some of the boundaries between different sediment types.

The 1989 USGS map was later extended to the southwest (Poppe et al. 1994) to investigate the region from offshore Connecticut to North Carolina. The western extension evaluated the same sediment data base consisting of 11,000 samples in the region. "Although all of these analyses were considered when the textural distributions were interpreted, only selected representative sample localities were plotted on the map." Furthermore, the authors stated that "because the true boundaries between sediment types are probably highly irregular or gradational and because the accuracy of the navigational systems used during the earlier studies is limited, all contacts should be considered to be inferred."

A significant revision of the basic map occurred in the Georges Bank area in 1993 (Valentine et al. 1993). The revisions were based on seismic reflection profiles, sediment texture analysis (306 samples), and on visual observations from submersibles. Valentine's study substantially altered the distribution of gravel pavement and gravely sand on the northeastern flank of Georges Bank (Fig. 46). In addition, the study (Valentine and Lough 1991, rev. 1992) showed the importance of these gravel pavements to herring, cod, and scallops. This is an area which has long been recognized as important lobster grounds.

Another region which has been significantly revised is Massachusetts Bay (including Boston Harbor) and the Cape Cod Bay area (Fig. 47). Massachusetts Bay (Knebel and Circe 1995 A and B) was subdivided into three different environments on the basis of 5 sidescan sonar surveys and high-resolution seismic profiles. Additionally, nearly 500 bottom samples and cores were further documented with bottom photos and video camera transects.

These sidescan sonographs are only capable of recording the amount of scatter which sound waves experience as they are reflected from the sediment-water interface. In contrast, the high-resolution "boomer" data can penetrate several hundred meters (approx. 1000 ft) below the sea floor and can distinguish individual layers of sediment.

Based on a combination of this data, Knebel's environmental classification consists simply of the following:

> Erosion or Nondeposition - (sediments are being removed and transported beyond the area) Seen as isolated reflections and patterns of strong back scatter.
>
> Sediment reworking - (sediments are being eroded and deposited locally) Seen as patterns with strong to weak back scatter.
>
> Deposition - (sediments are being laid down) Seen as patterns of weak back scatter.

Later, Knebel (Knebel et al. 1996) applied this same environmental classification scheme to the sediments of Cape Cod Bay. He is currently doing detailed work in Long Island Bay (Knebel, personal comm.).

In an effort to achieve some level of uniformity in the current maps, we have further defined these environments in a general way utilizing sediment texture diagrams and descriptions as a guide. This guide was then used in conjunction with previous maps and bathymetric contours to allow the following inferences:

Patterns with isolated reflections - (predominately rocks, boulders and cobble).
Patterns of strong back scatter - (mostly sandy gravels and gravely sands).
Patterns with strong to weak back scatter - (sands and silty sands).
Patterns of weak back scatter - (mud, sandy mud and silt).

Recently, major revisions were made in the substrate maps of coastal Maine (Kelly et al. 1996) also based on the results of sidescan sonar (3358 km or 1800 nautical miles) and boomer seismic (5011 km or 2700 nautical miles). This data was "ground checked" with 1303 bottom grab samples. For areas that were not directly imaged by sidescan sonar, the authors state, "contacts between these geologic units was inferred based on bathymetry and other information." Once again it was occasionally necessary to extrapolate (estimate) from sonar images to the substrate type. Moreover, the transfer of these detailed maps (1:100,000) to a larger scale (1:1,000,000) is not a precise operation given the uncertainties of paper stretch and the differences in map projections. For these reasons, the contacts were sometimes modified by extrapolating (extending) the coastal rocks delineated on the Surficial Geologic Map of Maine (Thompson and Borns 1985) and the Bedrock Geologic Map of Maine (Osberg et al. 1985) into the shallow offshore margin.

Finally, slight adjustments were made to the sediment maps inshore based on a set of Bathymetric Fishing Maps (NOAA 1986, NOAA 1987) which include sediment information compiled from the National Ocean Service (NOS) hydrographic survey. Other changes implemented near shore were supported by more than 150 color aerial photographs (Patey 1996) taken along the coast from Connecticut to Maine between the months of May and September 1995. These photos make it possible to compare surface relief and geologic character with bathymetry and marine sediment distribution.

While no single set of maps can reasonably convey all of the intricacies of the sea floor substrate, every effort has been made to make these as timely as possible. Special care was taken to ensure that many of the significant advances made in the field in the last decade were included and, where possible, that more than one source was considered for each contact.

➢ Distribution and Frequency of Environments

In the literature, the distribution and frequency of substrate environments are rarely discussed. Most of the serious work has been done only in the last decade and much is conflicting depending on the particular stretch of shoreline selected. These examples illustrate the tremendous differences in substrate frequency which have so far been documented.

Perhaps one of the most detailed reviews of the Gulf of Maine environments is contained in the Environmental Atlas (Conkling 1995) which attempts to use the latest satellite imagery and thematic mapping to identify particular habitats. Just this month, these satellite techniques were expanded upon (Platt 1998) and applied to the bays and estuaries from Cape Cod to Canada. Clearly these techniques coupled with traditional ground surveys have the potential to revolutionize our understanding of the Gulf of Maine habitats. All that is needed is enough time and effort to extend these detailed area maps into a Gulf-wide framework, which could be of real value to all fishermen in the region.

The first comprehensive study of environments of the entire Maine coastline was recently done as part of the state regional mapping project (Kelly et al. 1996). A portion of this map in Penobscot Bay (Fig. 48) was recently reprinted (Platt 1998). Their detailed substrate maps of the coast of Maine reveal the following distribution:

Rocks - The rocky seabed is the most abundant sea floor type and comprises 41% of the inner continental shelf.

Mud - Muddy areas are the next most common (39%) and are the dominant sea floor material in all near shore areas with the exception of southern Maine where rock and gravel predominates. It is also the major deep-water surficial material.

Gravel - Gravely areas comprise 12% of the coastline and are concentrated off Kinnebec Mouth where deltaic sediments are exposed, off Wells and Sacco Bays near reworked glacial moraines, and near the Canadian border.

Sand - Sandy areas-represent only 8% of the substrates and are primarily situated along southern Maine beaches and in the Kinnebec delta. They are often patchily distributed around the 50-60 m (165-200 ft) depth near the lowest stand of sea level since the last ice age.

An earlier localized survey along a mere 60 km (37 miles) of Maine coastline showed 11% of the substrates surveyed was cobble, 24% was sediment (presumably sand and mud) and 65% was ledge (presumably rocky shoreline) (Wahle and Steneck 1991).

Of the substrates surveyed in Canada along the Baie de Plaisance, Gulf of St. Lawrence, 91.2% were sand, 7.6% were deep (greater than 5m or about 15 ft), rocky bottom and 1.2% were shallow (less than 5m or about 15 ft) rocky bottom (Hudon, 1987).

In Massachusetts, recent substrate surveys have been completed by the USGS (Knebel et al. 1995A, 1995B and 1996).

Boston Harbor

Erosion or Nondeposition - (20%)
Sediment reworking - (29%)
Deposition - (51%)

Massachusetts Bay

Erosion or Nondeposition - (71%)
Sediment reworking - (26%)
Deposition - (3%)

Cape Cod Bay

Erosion or Nondeposition - (29%)
Sediment reworking - (17%)
Deposition - (54%)

Stellwagen Basin

Erosion or Nondeposition - (16%)
Sediment reworking - (14%)
Deposition - (70%)

*See section above for interpretation from environment to rock type.

The USGS mapping projects indicate that the important gravel/cobble substrate usually makes up less than 15% of the coastal environment. These percentages decrease rapidly away from the coastline.

Offshore most of the gravely areas are associated with shoals or canyons. Even the submarine canyons mainly have thin gravels distributed only on the east side of the canyon walls (see Fig.41). Away from the shallows and the submarine canyons, the gravels appear to be quite rare.

This has serious implications for the lobster because they are increasingly competing for preformed shelters in this size range. The scarcity of these rocks in the basins could partially explain why lobstermen report finding more lobsters on "soft bottom" than they did just a few years ago.

➢ *SHELTER DEPENDENCY SCENARIO*

It has been reported that a lobster's dependence on habitat decreases as it gets older and larger (Wahle and Steneck 1992). This is only partly true, for while the adult lobster possibly needs less protection from predators, the shelter becomes an essential ingredient for reproduction. To fully grasp the importance of shelter and the changing role it plays with growth, it is necessary for the reader to put him- or herself in the position of the lobster and to begin to "think like a lobster." The following hypothetical narrative is but one habitat scenario for a dominant male and assumes optimum conditions at nearly all life stages:

Hatched in Atlantis Canyon in mid-June, the larva's first instinct is to swim to the surface. The pueblo village rapidly disappears into the depths as thousands of other Stage I larvae fight to reach the surface before being eaten. Once at the surface, its bluish outline is practically invisible and it needs only to escape the mouths of birds and fish. Its survival at this point depends on getting close to shore. Fortunately, at this time of year, the current is generally shoreward and the wind is from the south.

In three days, the larva molts to Stage II and another 3 days brings on another molt into Stage III. By this time, the larva has moved nearly 80 kms (about 50 mi.) to the north and slightly west of the canyon. Another 4 days and dramatic changes take place as the larva molts into a Stage IV postlarva. Now the postlarva can begin swimming during daylight at about 18 cm/sec (about 7 in/sec). It begins swimming northward and partially counters the westward current (see Katz et al. 1994).

With the metamorphosis comes a change to a brownish color and suddenly the postlarva is highly visible and vulnerable. Fortunately, a small clump of seaweed floats by as it moves shoreward and the postlarva swims toward it for cover. Approximately 2 days later, the postlarva is compelled to begin bottom-seeking behavior. During its first few dives it encounters a thermocline and as the temperature drops rapidly it quickly heads back to the surface.

As the shoreline is approached, the thermocline dissipates and the postlarva is able to swim to the bottom. At its first touchdown it encounters only clay. Somehow, it knows that it would take more than 30 minutes to make an adequate burrow in clay and within 15 minutes it is likely to become a meal for a passing cunner or other fish.

Three days later it encounters a sand bottom and it senses a cunner in the vicinity. It knows that sand offers little protection and if it is forced to burrow there, it will soon be exposed and eaten. It lifts off and begins frequent probing of the bottom. Another three days and it is becoming desperate (see Boudreau et al. 1993).

It is now nearly halfway through Stage IV and it needs to find a hiding place so that it can molt again. At last, it reaches a gravel substrate just off the coast of Rhode Island and within 30 seconds chooses a crevice. Immediately, it begins burrowing and probing to make a suitable home while it is suspension feeding. At this stage, the postlarva is still quite small (5 mm or about 0.2 in CL), but it still requires a minimum sediment size (see Fig. 4C) of 21 mm or about 0.8 inches (small pebbles) in order to accommodate its body size (see Wahle 1992). The lobster will reach a size of at least 12-14 mm (about 0.5-0.6 in) CL in the first summer and over winter in Stage IX-X (see Lavalli, 1991). During this period the lobster will not leave its shelter.

During the second year, it will grow to as much as 25 mm (~1 in) to an emergent and possibly vagile juvenile, depending on water temperature. At this size, it will require a substrate of 100 mm or about 4 in (small cobbles) to provide the same level of protection. It will then have to emerge in search of additional food and a larger shelter. It selects this shelter carefully so that it will have maximum access to other environments and resources within a few meters (yards). By this phase, it will probably only molt in spring and autumn.

At about 40 mm (1.6 in) CL the lobster is an adolescent and begins to feel mature. It becomes active at night and may pointedly seek out other lobsters. It participates in so-called "boxing matches" with other males (and some females), but almost invariably a 5% weight difference results in the dominance of the heavier lobster (Bushman and Atema 1993). Since there is not a dramatic difference in dimorphism between male and female claws yet, males have only a slight size advantage over females, but this is usually enough to establish dominance.

The adolescent lobster spends a considerable amount of time investigating other lobster shelters and in turn protecting his own. He might roam as much as 300 m (roughly 1000 ft) in a day. He is frequently evicted and must find other shelters for protection during molt. Since only existing shelters of about 170 mm or about 6.7 in (medium to large cobbles) will suffice to protect its entire body, he must prepare his own enclosure if none are available.

In an effort to find available shelters, he may be driven into Narragansett Bay. Here the lobster encounters a bottom composed of clayey sand which he can burrow into and cover over during winter. The other lobsters in the area are mostly weak or wounded and he can sometimes establish dominance over a few males for a short period until a larger adolescent moves in. In this stressed environment, food is at a premium, so the bait of a lobster trap might be very attractive (see Jury et al. 1994a).

By age five, the lobster only needs to molt about once per year. Somewhat immune to predation after 60 mm (2.4 in) CL inshore, the mature lobster is tempted by the migrating females and follows them into deep water. As he reaches the shelf edge, he soon realizes that he is now susceptible to larger predators and will once again begin searching for shelter (see Wahle and Steneck 1992). Soon the lobster finds itself in one of the offshore canyons again. The eastern wall is steep, but is layered with gravel pavement and boulders and there appear to be many available clay burrows.

No sooner has he succeeded in evicting a crab from one of the shelters, but the lobster is then evicted by one of the larger males in the area. He moves a little farther away and occupies a less attractive shelter. It is large enough for one lobster, but is not capable of being enlarged for two.

For several years, the lobster engages in mock battles with other lobsters of his approximate size. However, win or lose, he is still subordinate to the larger males. As the now mature lobster grows beyond 110 mm (4.3 in) CL, he finds that he can now devote much of his time to acquiring and keeping a mating shelter. He has seen how the females are attracted to large burrows with at least two entrances and access to currents for carrying their scent. He builds several burrows, but is only able to attract inseminated females. Then, for some reason the dominant male is suddenly gone.

He fights off a few younger males and occupies the prized shelter and prepares for company. He advertises his presence by releasing his urine inside and at the entrance and soon one of the smaller females begins probing the entrance. He waits and soon more females approach.

Finally, after 10 years, he is in a position to reproduce. He has outlived almost all of his other hatchlings which were either eaten by predators or succumbed to other lobsters after they molted. He has beaten all of the odds and now his sperm will fertilize hundreds of thousands of eggs. His instincts for survival and genes for resistance and growth will be passed on to later generations, which should insure that at least a few would survive to take his place.

12). LOBSTER DISTRIBUTION MAPS

Finally, we come to the goal of this exercise, which is to understand the spatial and temporal (place and time) distribution of lobsters in relation to the available substrates and possible Essential Lobster Habitats. To accomplish this goal several different approaches were attempted, but all were eventually shown to have severe limitations. Obviously, the best source of information on where lobsters are present during their various life stages is the lobstermen themselves. Of course there will always be a slight difference of opinion as to who actually qualifies to represent the legitimate lobstermen.

Knowing the reluctance which lobstermen understandably show about revealing the positions of their favorite lobster grounds, we adopted a different strategy. First, we tried to determine the least likely places where lobsters would be found. This effort failed due to the limited time constraints on the project.

Next, we attempted to determine where the lobstermen thought that some of the historic breeding grounds were located and where some of the rare habitats such as clay pipe used to be found. We got the same negative result.

We attempted to determine trap density along the coast based on aerial photos. Unfortunately, we soon realized that some lobstermen leave their traps for long periods in areas they do not fish. They also sometimes leave traps on lobster grounds in order to preserve their territory and prevent others from fishing there.

Lastly, we tried to determine which areas used to be considered highly prized lobster grounds, but now are no longer as attractive. Although we tried several methods from questionaires, to oral histories to posting maps, none were successful in the time allotted.

Another objective for this report was to involve several academic institutions and scientific laboratories in the data collection. This was to ensure that the latest findings were incorporated into the study. This objective was only partially met by focusing on currently published articles and relying heavily on personal contacts and the Internet. Also, several Lobster Summit proceedings were reviewed to fully understand the thrust of current (as yet unpublished) research projects. Later, personal contacts with other researchers active in the field proved invaluable in the final draft of this report.

Additionally, it would have been desirable to work with agencies which are responsible for management of the lobster fishery such as ASMFC, NMFS and NEFMC. Undoubtedly, their resources and input could have provided useful insights into these problems. However, direct contact was discouraged until the project was initially completed.

In spite of these handicaps, a picture of adult lobster distribution seems to be emerging from the data at hand. Put simply, lobsters appear to concentrate at the edges of habitats and near the substrate contacts. The evidence comes from the published NMFS trawl survey data. Of course, it is well known that the trawl surveys do not fully sample all habitats. They are limited by shallow depths, do not sample coastlines, and tend to avoid so-called "hangs" and "hard ground." Furthermore, trawling is impossible in areas where there are too many traps. Nevertheless, when all of these factors are taken into consideration, an adult lobster distribution is revealed that appears surprisingly predictable based on the substrate maps.

One of the earlier published maps of lobster distribution (Fig. 49) was compiled by NMFS as part of a much larger study of Fish Distribution in the NY Bight Region (Grosslein and Azarovitz 1982). Since 1967, continental shelf waters more than 27 m (about 89 ft) from Nova Scotia to Cape Hatteras have been surveyed at least twice each year in spring and autumn. To provide a more generalized picture of density distribution for autumn and spring, the 1973 and 1974 offshore data were combined in a single plot. The survey area was subdivided into 76 different regions or "strata" based on geographic and hydrographic factors. Trawl stations were randomly selected in each stratum, with approximately one station for every 1,000 sq. km (300 sq. nmi). Nets used were modified commercial otter trawls designed for fishing on the bottom. There is no indication that the particular habits of lobsters were in any way considered in this sampling program.

These published maps reveal only part of the story since they show only where lobsters were retrieved rather than where they were absent. Still, when these maps are overlain to the revised substrate map, there is a general correspondence between the relative lobster distribution in spring and the coarser sediment contacts. This pattern is repeated in autumn when lobsters move across the Georges Bank into relatively warm shoal waters. While it is dangerous to generalize from such a large-scale biased survey with fewer than 150 points of control, these results are intriguing and warrant further investigation.

The other published NMFS trawl survey map (Fig. 50) was included in the Atlas of the Georges Bank (Backus 1987). Again the trawls were random with no attention given to American lobster sites. Here we have a compilation of several years of surveys conducted between 1968 and 1981. We also have more than 200 points for two seasons where lobster were retrieved (ranging from 0.1-10 kg or 0.22-22 lbs in landings). Perhaps of greater importance are the nearly 300 control points for each season where no lobsters or at least less than 0.1 kg (0.22 lbs.) were found. This allows us to overlay the lobster distribution maps to depth and substrate maps and begin to investigate areas where lobsters are actually scarce.

From the overlays we see that no significant numbers of lobsters were taken during the fall in the vast central area of the Gulf of Maine. In this region covering an area of more than 40000 sq. km (nearly a million acres) over 50 trawl attempts were made without success. The situation is similar in the spring with only two trawls recovering lobsters in the region. When we examine the area carefully we find that depths generally range from 150-200 meters (roughly 500-650 ft). The substrate map shows that the bottom consists mostly of fine-grained sediments including sand silt and clay with an abundance of sandy silt and clayey silt. Although a few shallow ledges characterized as gravely-sand appear to have been sampled, no lobsters were recovered in the trawls.

Looking more closely at the Georges Bank area, we find the expected concentration in both seasons along the shelf edge, but find that very few lobsters are encountered on the central bank area in spring. In the fall, there are several more successful trawls, but these appear to be localized around a few gravely sand areas shown on the south side of the bank.

Returning to the 1973 maps, the same gap in the central Gulf of Maine is present, with no lobsters obtained in fall and only two successful trawls in spring. On Georges Bank we find the same relationship to the gravely areas.

The agreement is uncanny between two sets of data obtained nearly a decade apart. From this trawl data, it appears that lobsters are more frequently found on the boundaries between two different substrates. It has previously been suggested that local population density may correspond with the availability of shelters (Bologna et al. 1993). Additional evidence indicates that boulder shelters are also a necessary ingredient (Hudon and Lamarche 1989). These findings suggest that the American lobster may be a key indicator species, which is much more laterally restricted than some of the literature would indicate. This could either be due to the lobsters' preference for maximum information and environmental choices (as we saw with kelp) or it could be due to sample bias.

Unfortunately, no further conclusions can be drawn from such small maps, but it is imperative that this overlay procedure be duplicated with full-scale maps and a more complete and current database. There are anecdotal reports that lobsters in recent years have become more concentrated in soft bottom areas, but maps to support this argument have not yet been published. If possible, these types of maps and input from lobstermen should be integrated into a GIS (Geographical Information System) and then statistics could be applied to determine significant correlations. Only then will we begin to see to what extent lobsters have become dependent on a few areas of prime habitat in the offshore region for their future survival.

13). MAPS OF THE LIFE HISTORY STAGES

➢ ***Larval-(egg) STAGE I Distribution***

As stated previously, eggs hatch immediately upon release so only the Stage I larvae would be expected to reach the surface. Unfortunately, no comprehensive maps of Stage I larvae distributions have been published. It is therefore necessary to infer Stage I larval distribution from local studies and to show where similar oceanographic conditions are present. For inshore sampling of Stage I larvae, we rely largely on the work of Fogarty and others (1983). For the offshore area, we only have published larval maps near the canyons (Katz et al. 1994).

In the offshore region, the Stage I map (see attached folder) highlights the outer shelf and upper slope which contains the canyons and the areas between them. We have no data for the area south of Block Canyon, but it is assumed that the offshore populations contribute some larvae in this area as well. In addition, it is generally believed that Georges Bank, Browns Bank, and the Bay of Fundy contribute significantly to the inshore population (Cobb and Wahle 1994)

Inshore, Fogarty and others (1983) have shown significant Stage I larvae at Block Island Sound, Buzzards Bay, Cape Cod Bay, Penobscot Bay and at least one sample at Hampton-Seabrook. Some of these maps are detailed enough to show rapid decreases away from the estuaries. Other large estuary systems are believed to contain Stage I larvae, but the work has not yet been published.

➢ ***Post-larval-(larval) STAGE 1V Distribution***

For the map of the larval- postlarval distribution (see attached folder) we are left with a dilemma. We can either designate the entire Gulf of Maine as EFH based on the planktonic distribution of Stage I, II, III and part of Stage IV or attempt to map only postlarval distribution. We have chosen to map Stage IV settlement because it corresponds directly to the habitats which need to be protected for the continued growth and recruitment of the species.

The postlarval map once again highlights the areas inshore where Stage IV larvae have been sampled directly by Fogarty and others (1983) and Katz (1984). Here we have combined the postlarval distribution at the surface with gravel and gravely sand substrates which are preferred for settlement. In Maine, we have included rocky shores where algae may have been established. We have also utilized the recent work in Penobscot Bay (Steneck and Wilson 1998). Finally, we have suggested that some postlarvae may settle on Stellwagen Bank, but we know of no studies to support this possibility, although current studies by Wahle (personal communication) may soon answer this question.

➢ ***Juveniles***

The map of juvenile distribution (see attached folder) encompasses shelter-restricted, emergent, and vagile juvenile phases. Because it is a composite of three different phases it naturally includes many habitats. These occur primarily among cobbles, rocks on sand, and peat reefs.

Work done at Great Bay Estuary (Brown et al. unpub.) provides a model for juvenile distribution in the mouths of estuaries. Long Island Sound is assumed to be a major area for juveniles, but we do not have access to detailed data for this region. Also, while the precise location of peat reefs is unknown, the distribution of salt marshes (which may contain peat reefs) have been mapped for Cape Cod and 17 estuarine systems. Gravel, gravely sand and rocky substrates have also been included in this distribution.

Finally, the outer shelf-upper slope has been highlighted including those areas which may contain a clay base in this setting. These clay areas may contain important clay depressions or mud anemone habitats (Lawton and Lavalli 1995). Clay pipe areas should also be added to this distribution as they are revealed.

- ***Adults***

The map showing the distribution of adults is perhaps the most uncertain. This map shows the most important habitats for both adolescent and adult lobsters (Lawton and Lavalli 1995). While many have argued that adult lobsters are ubiquitous, there is little published evidence to support their widespread occurrence on unfettered, sandy bottom on the shelf, except during times of migration.

Offshore, this map highlights lobster occurrence on the outer shelf-upper slope regardless of substrate. It also focuses on the gravely sand areas on the banks and the clay regions in the basin interiors.

Inshore, adult lobsters are likely to utilize all substrates, at least temporarily. Until information is forthcoming on where adult lobsters are not found inshore, it is prudent to show all habitats. This includes interior estuaries and salt marshes. Based on the limited data we have, island margins appear to be particularly important.

14). HUMAN IMPACTS ON HABITAT

- ***Habitat Destruction***

Any discussion of human impacts on marine habitats is inherently controversial. The only thing most people can agree on is that different habitats are impacted differently. In an effort to quantify the impact of fishing activities on habitats, Peter Auster has prepared a conceptual model (Auster and Langdon 1998). The graph (Fig. 51) shows the relative level of complexity of various substrates and how that changes with increasing fishing effort. They showed that piled boulders are most complex and are the most sensitive to fishing effort. Next comes dispersed boulders and cobbles followed by pebble-cobbles with epifauna. Bedforms such as sand and silt are not surprisingly shown as the least complex and the least sensitive to alteration. Significantly, they have not included any mention of bedrock or rocky ledges and shorelines. Intuitively, these also would be very insensitive to fishing effort regardless of their complexity.

Auster and Langdon (1998) provide a map of nearly 15,000 trawl and scallop dredge tows (Fig. 52) conducted between 1989 and 1994. When this map is overlain to substrate, it is clear that the gravel bottoms are being heavily trawled. If this map is representative of commercial tows in general, then we should find evidence of reduced complexity in the most heavily towed gravel and cobble areas.

This is precisely what Valentine and Lough (1991) have documented in photos of eastern Georges Bank (Fig. 53). Untrawled areas with gravel pavement show abundant worm tubes and other attached organisms. In trawled areas the rocks are bare and both complexity and productivity is decreased.

Cooper and others (1987) have shown similar effects in the submarine canyons where blocks of the thin gravel pavement have been knocked off the walls and fallen to the canyon floor

Habitats on Stellwagen Bank are impacted to a lesser extent due to differences in substrate. The sidescan sonar images (Fig. 54A and 54B) reveal numerous otter trawl and dredge marks on the sandy bottom, but these activities apparently have little impact on the habitat complexity.

From these examples, we can cautiously conclude that bottom trawling has a significant impact on lobster habitats in coarse-grained sediments like boulders, cobble and gravel, but little effect on finer grained sediments. However, we must not ignore the potential for damage to extremely fragile habitats like clay pipe and anemone burrows in the mud/clay setting. This still leaves a few habitats where bottom trawling probably does little damage.

Adult lobsters are also subject to man's influence. Lobsters have historically been known to live for more than 30 years. Even under contemporary patterns of commercial exploitation, lobsters up to 217 mm (about 8.5 in) CL and weighing about 9 kilos (nearly 20 lbs.) have been encountered in shallow water during the summer months.

Lobsters are sensitive to chemicals and have been known to vacate areas that have become polluted. However, not all of these impacts are negative. Some of the largest lobsters have been known to occupy man-made shelters such as discarded cans and barrels.

Other important human activities which 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 which results in raw sewage discharges during times of overflow. All of these pollution sources can have a tremendous impact on water quality, habitat preservation and ultimately human health. These problems can be multiplied when the contaminants get into the sediments and then are disturbed by dredging. When the contaminants are suspended in the water column they become available for uptake by many species (including lobsters) and can accumulate throughout the food chain.

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" (Potter and Elner 1982).

Considerable research has already 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." Some of these tests resulted in the death of adult lobsters within hours. 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 (about 0.04 in) covering of drilling mud may cause increased exposure to predators and currents, resulting in the substrate becoming unsuitable for lobster settling and survival."

Recently, concern has been raised about the effects of sewage outfall pipes on lobsters. As we have seen, environmental conditions which are not toxic to lobsters can still cause them to shift or vacate an area. These include changes in temperature, salinity, currents, substrate, pH, dissolved oxygen, nutrients, pesticides and other contaminants. Much work is still needed to understand exactly why lobsters have apparently abandoned certain areas impacted by man.

- Habitat enhancement

There have been few documented examples of lobster habitat enhancements in the Gulf of Maine, but there may yet be significant potential. We have already mentioned the favorable results obtained by planting artificial kelp beds. Similar results were obtained when artificial shelters made of PVC pipe or concrete blocks were positioned on the sea floor (Ojeda and Dearborn 1991). So far, the evidence seems to indicate that these methods merely serve as gathering points for lobsters in the surrounding area. Many believe that overall lobster density is not increased, but this may be an oversimplification.

Anecdotal evidence of lobsters being attracted to discarded rubble may point the way forward. This enhanced image on the flank of Stellwagen Bank (Fig. 55) purportedly captures a boulder pile that was dumped some time ago. Lobstermen now report good catches in this vicinity. If lobsters do concentrate on the edges of habitat boundaries, it is likely that here they would be afforded additional protection from predators. It is therefore reasonable to assume that their overall survival rate would increase. Furthermore it is possible that some artificial lobster shelters might be adapted to increase reproductive success as well. In addition, we have just begun to explore the possibility of artificial clay pipe habitats. Clearly more work is needed in this area before any firm conclusions can be drawn.

15). INTERPRETATION OF CATCH DATA

According to the most recent stock assessment summary SAW-22 (NEFSC 1996) total landings have more than doubled since 1978, reaching an all-time high of nearly 32,000 metric tons (over 66 million pounds) in 1994. This increase in landings has occurred over a wide geographic area, covering a wide range of habitats and extending throughout many fisheries and management regimes. Lobster size is decreasing, with the mean size of lobsters landed within one or two molts of the minimum size regulation. This indicates that the fishery is still dependent on newly recruited animals, which have just grown into legal size. These are general concerns for lobster management.

From a habitat point of view several trends are particularly alarming:

Firstly, the data shows an over-reliance on statistics and modeling with little or no spatial information. The result is that while average trends in overall productivity may be compared by region, there is virtually no monitoring of changes occurring on a sub-regional scale. This means that a local stock could collapse due to habitat degradation and possibly create a cascade effect, which would not be recognized until it is too late.

Secondly, landings are concentrated in a few areas. Landings in Maine constitute about half of the total, with about 25% occurring in Massachusetts. Overall, the coastal fisheries accounted for 86% of US landings in 1993. The inshore lobsters are competing for a limited number of coarse substrates for their protection. This very heavily fished inshore population also depends critically on the larval subsidy provided from the offshore and canyons areas. The recent expansion of fishing into the offshore area could prove a continuing threat to the entire population. It is therefore prudent that the level and pattern of offshore exploitation should be controlled.

Furthermore, some areas are being particularly hard hit by a concentration of traps. For example, in 1996, Boston Harbor and its surrounding area supplied nearly 2 million lbs. (approx. 22% of commercial landings in territorial Massachusetts). Not enough has been done to monitor sensitive habitats in these vital areas or determine the long-term effects of pollution on lobsters in the harbors.

Thirdly, landings are increasingly being concentrated during a critical few months of the year. In 1996, approximately 82% of landings within the territorial waters of Massachusetts occurred between July and November with concentrated landings in September and October. This is the critical time period after the lobsters have molted and just before females extrude their eggs (which then affords them protection against fishing). If similar compression of the season are occurring in other regions, this places an additional burden on the habitats and the resource to recover before the next disruption.

Lastly, it is well known that a significant proportion of lobsters are landed before they reach sexual maturity. This compresses spawning potential into an increasingly narrow size range and presumably age range as well. The SAW 22 panel cautions that "at low levels of egg production … stock collapse could come quickly and without warning."

All of these warnings have been heard before. What is not fully appreciated is the fact that we are placing ever more reliance on a shrinking size range, which increases the competition for particular environments. Other heavily fished species may become equally compressed which compounds the problem of available shelters. If these laterally restricted habitats do not currently represent an ecological bottleneck, they soon will. The rapid changes that are occurring in these sensitive and complex ecosystems create an ever-shrinking safety zone for the American lobster. If we do not begin to identify, delineate, and preserve these habitats, we may find that we are trying to save a species which has nowhere left to hide.

16). CONCLUSIONS

Most of the early work on lobsters involved mortality and lobster tolerances and not optimum environmental conditions and preferences.

Lobster habitat preferences are generally dictated by their biological drive to maximize growth, survivability, and reproductive potential. Environmental preferences control their selection of habitat much more than their tolerances to various conditions. Lobsters frequently change habitats as they grow in order to utilize the full range of available shelters and environmental niches.

It has generally been thought that a lobster's dependence on shelter decreases as it grows, but this is true only with regard to predators in shallow inshore regions. Shelter is an essential part of the mating ritual; it is also an essential escape from predation by larger, offshore fishes. Mature lobsters rely heavily on shelters for protection during the molt period and for establishment and maintenance of dominance and for courtship.

Although American lobsters can be located in any habitat at any stage of their life cycle, they are not equally likely to be found in a given habitat during a particular period. There are vast areas where lobsters are rarely captured in trawls.

Published trawl surveys are inadequate to accurately delineate the distribution of the American lobster. Every effort should be made to utilize satellite positioning information with these surveys and to supplement these data with reports from lobstermen.

Bottom temperatures appear to determine habitat preferences and migration patterns of the American lobster. Preliminary work indicates that the mean bottom temperature in the Gulf of Maine is increasing. Fluctuations in the volume of slope water entering the Northeast Channel may be partly responsible for the general temperature trend.

Marine habitats are made up of a near infinite variety of oceanographic, biologic and geographic factors. Estuaries and continental margins (especially canyons) are complex ecosystems that combine a number of known lobster habitats. These environments are fragile and subject to rapid changes due to human impacts

Mature females normally lose 30-50% of a clutch during the long brooding interval of 9-16 months. Poor environmental conditions or stress may lead to significant further losses. Thus identification and protection of brooding habitats should be a priority.

Optimum habitats are much more limited in aerial extent than previously thought. There is some evidence to suggest that lobsters prefer the boundaries of two different habitats in order to maximize food and shelter opportunities, as well as to maintain maximum flexibility under changing environmental conditions. If this is the case, then it further reduces the amount of optimum real estate on the sea floor.

17). RECOMMENDATIONS

The "boundary effect" present around seaweed should be investigated thoroughly with regard to other habitat boundaries. In particular, comparisons should be made of how lobster densities change with differing sizes, shapes and types of habitat.

In future, descriptions of marine sediments must be as specific as practical, especially with regard to the largest particle sizes. These gravel, pebble, cobble and boulder substrates are highly variable and are too important as Essential Fish Habitats to lump together as one convenient gravel classification.

Greater emphasis should be placed on describing and mapping bottom environmental conditions regionally, not just for lobsters, but for the many other important species that utilize and must adapt to bottom conditions during part of their life cycles. State of the art mapping techniques are currently being applied to the most critical areas, but an all out effort is needed to fit these local areas into a larger picture of substrate distribution.

New research is needed on lobster communities in the wild with particular emphasis on how communities restructure when members are removed. We need to better understand how lobsters socially interact at the community level and what effect migration has on this interaction.

Additional research is needed to determine the maximum density of dominant males in a given habitat. Much can be learned by observing how many shelters are twice the size of the mature lobster. These are the only shelters where the adult lobsters are likely to mate. It should be possible to selectively remove the large dominant male in a test situation to see how the largest females respond.

Future work on habitats and substrate should be done in conjunction with Federal and State agencies, academic, and private institutions. It should utilize Geographical Information Systems (GIS) and satellite mapping techniques.

Serious consideration should be given to protecting large lobsters in order to maximize reproductive potential and protect the gene pool. If large lobsters do not reproduce, the species will not be passing on its strongest, most survivable, traits. However, protection of large lobsters should not be viewed as a panacea for dealing with overfishing and habitat loss.

REFERENCES

Aiken, D.E. and Waddy, S.L. (1986). Environmental influences on recruitment of American lobsters (*Homarus americanus*): A perspective. Can. J. Fish. Aquat. Sci. 43: 2258-2270.

Atema, J and Voigt, R. (1995). Behavior and Sensory Biology. *In* "Biology of the Lobster *Homarus americanus"* (edited by J.R.Factor), Academic Press, NY. pp. 321-329.

Auster, P J. and Langton, R.W. (1998). The Indirect Effects of Fishing. (In Preparation).

Backus, R.H., editor (1987). "Georges Bank," MIT Press, Cambridge, MA

Barshaw, D.E. (1989). Growth and survival of post-larval lobsters, *Homarus americanus*, on a diet of plankton. Fish Bull. 88: 415-417.

.Barshaw, D.E. and Bryant-Rich, D.R. (1988). A long-term study on the behavior and survival of early juvenile American lobster, *Homarus americanus*, in three naturalistic substrates: eelgrass, mud and rocks. Fish. Bull. 86: 789-796.

Barshaw, D.E. and Lavalli, K.L. (1988). Predation upon postlarval lobsters *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crabs *Neopanope sayi* on three different substrates: eelgrass, mud and rock. Mar. Ecol. Prog. Ser. 48: 119-123.

Bologna, P.A.X., Steneck, R.S. (1993). Kelp beds as habitat for American lobster *Homarus americanus*. Mar. Ecol. Prog. Ser. 100: 127-134.

Boudreau, B., Bourget, E.; Simard, Y. (1993). Effect of age, injury, and predator odors on settlement and shelter selection by lobster *Homarus americanus* postlarvae. Mar. Ecol. Prog. Ser. 93(1-2): 119-129.

Boudreau, B., Simard, Y.; Bourget, E. (1992). Influence of a thermocline on vertical distribution and settlement of post-larvae of the American lobster *Homarus americanus* Milne-Edwards. J. Exp. Mar. Biol. Ecol. 162(1): 35-49.

Botero, L. and Atema, J. (1982). Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. J. Crust. Biol. 2(1): 59-69.

Bushman, P.J. and Atema, J. (1997). Shelter sharing and chemical courtship signals in the lobster *Homarus americanus*. Can. J. Fish. Aquat. Sci. 54: 647-654.

Campbell, A. (1990). Aggregations of berried lobsters (*Homarus americanus*) in shallow waters off Grand Manan, Eastern Canada. Can. J. Fish. Aquat. Sci. 47: 520-523.

Campbell, A. (1991). Juvenile *Homarus americanus* studies from McNutt Island, Nova Scotia. J. Shellfish Res. 10(1): 283-284. Abstract Only.

Capuzzo, J.M., Lancaster, B.A. (1979) Some physiological and biochemical considerations of larval development in the American lobster (*Homarus americanus*). Milne Edwards. J. Exp. Mar. Biol. Ecol. 40: 53-62.

Charmantier, G., Charmantier-Daures, M. Bouaricha, N., Thuet, P., Aiken, D.E., and Trilles, J.-P. (1988). Ontogeny of osmoregulation and salinity tolerance in two decapod crustaceans: *Homarus americanus* and *Penaeus japonicus*. Biol. Bull. 175: 102-110.

Cheng, J.H., and Chang, E.S. (1994). Determinants of postmolt size in the American lobster (*Homarus americanus*). II. Folding of premolt cuticle. Can. J. Fish. Aquat. Sci. 51: 1774-1779.

Cheng, J.H., and Chang, E.S. (1994). Determinants of postmolt size in the American lobster (*Homarus americanus*). I. D_1^3 is the critical stage. Can. J. Fish. Aquat. Sci. 50: 2106-2111.

Cobb, J.S.; Gulbranson T.; Phillips, B.F.; Wang, D; Syslo, M. (1983). Behavior and distribution of larval and early juvenile *Homarus americanus*. Can. J. Fish. Aquat. Sci. 40(02): 2184-2188.

Cobb, J.S., Juinio, M.A. and Bengtson, D.A. (1991). Estimation of recent growth of field-caught postlarval lobsters from RNA: DNA Ratios. J. Shellfish Res. 10(1): 283-284. Abstract Only.

Cobb, J.S. (1995). Interface of ecology, behavior and fisheries. *In* "Biology of the Lobster *Homarus americanus*" (edited by Factor, J.R.), Academic Press, NY. pp. 139-151.

Cooper, R.A., and Uzmann, J.R. (1980). Ecology of juvenile and adult *Homarus americanus*. *In* "The Biology and Management of Lobsters" (J.S. Cobb and B.F. Phillips, eds.), Vol. II. Academic Press, NY. pp. 97-142.

Cooper, R.A., Valentine, P., Uzmann, J.R. and Slater, R.A. (1987) Submarine Canyons. *In* "Georges Bank" 1987. (edited by) Backus, R.H., MIT Press, Cambridge, MA. pp. 53-63.

Conkling, P.W., editor (1995). "From Cape Cod to the Bay of Fundy - An Environmental Atlas of the Gulf of Maine." The Island Institute, MIT Press, Cambridge, MA.

Cowan, D.F. (1991). Courtship and chemical signals in the American lobster. J. Shellfish Res. 10(1): 284. Abstract Only.

Cowan, D.F. and Atema, J. (1990). Moult staggering and serial monogamy in American lobsters, *Homarus americanus.* Anim. Behav. 39: 1199-1206.

Crossin, G.T., Saud A.A., Jury, S.H., Howell, W.H. and Watson, W.H. (1998). Behavioral thermoregulation in the American lobster *Homarus americanus*. Journal of Experimental Biology. 201(3): 365-374.

Dibacco, C. and Pringle, J.D. (1992). Larval lobster (*Homarus americanus*, H. Milne Edwards, 1837) distribution in a protected Scotian shelf bay. J. Shellfish Res. 11(1): 81-84.

Ennis, G.P. (1983). The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland near-shore area. Can. Tech. Rep. Fish. Aquat. Sci. 1138: 23.

Ennis, G.P. (1991). Egg production and recruitment in a Newfoundland lobster population: Is there a relationship? J. Shellfish Res. 10(1); 283-284. Abstract Only.

Ennis, G.P. (1995). Larval and postlarval ecology. *In* "Biology of the Lobster *Homarus americanus"* (edited by J.R.Factor,) Academic Press, NY. pp. 23-46.

Estrella, B.T. and Morrissey, T.D. (1997). Seasonal movement of offshore American lobster, *Homarus americanus* tagged along the eastern shore of Cape Cod, Massachusetts. Fish. Bull. 95:466-476.

Factor, J.R. (1995). "Biology of the Lobster *Homarus americanus*" Academic Press, NY.

Fogarty, M.J. editor, (1983) Distribution and relative abundance of American lobster, *Homarus americanus* larvae: New England investigations during 1974-79. NOAA Tech. Report NMFS SSRF-775: 64pp.

Hayden, A. (1996). "Eelgrass and Fisheries of the Gulf Of Maine". The Island Institute, Rockland, ME.

Harding, G., Kenchington, E., and Zheng, Z. (1993). Morphometrics of American lobster (*Homarus americanus*) larvae in relation to stock determinations in the Maritimes, Canada. Can. J. Fish. Aquat. Sci. 50(1): 43-52.

Harding, G.C., Kenchington, E.L., Bird, C.J., Pezzack, D.S. and Landry D.C. (1997). Genetic relationships among subpopulations of the American lobster (*Homarus americanus*) as revealed by random amplified polymorphic DNA. Can. J. Fish. Aquat. Sci. 54(8): 1762-1771.

Hudon, C. (1987). Ecology and growth of postlarval and juvenile lobster, Homarus americanus off Iles de la Madeleine, (Quebec). Can. J. Fish. Aquat. Sci. 44: 1855-1869.

Hudon, C. and Fradette, P. (1993). Wind-induced advection of larval decapods into Baie de Plaisance (Iles de la Madeleine, Quebec). Can. J. Fish. Aquat. Sci. 50(7): 1422-1434.

Hudon, C. and Lamarche, G. (1989). Niche segregation between American lobster *Homarus americanus* and rock crab *Cancer irroratus*. Mar. Ecol. Prog. Ser. 52: 155-168.

Incze, L.S. and Wahle R.A. (1991). Recruitment from pelagic to early benthic phase in lobsters *Homarus americanus*. Mar. Ecol. Prog. Ser. 79: 77-87.

Jamieson, G.S., Stone, H., and Etter, M. (1982). Predation of sea scallops (*Placeopecten magellanicus*) by Lobsters (*Homarus americanus*) and Rock Crabs (*Cancer irroratus*) in underwater cage enclosures. Can. J. Fish. Aquat. Sci. 39, (3): 499-505.

Juinio, M.A.R. and Cobb, J. S. (1994). Estimation of recent growth of field-caught postlarval American lobsters, *Homarus americanus*, from RNA: DNA ratios. Can. J. Fish. Aquat. Sci. 51: 286-294.

Jury, S.H., Kinnison, M.T., Howell, W.H. and Watson, W.H. III. (1994a). The effects of reduced salinity on lobster (*Homarus americanus* Milne-Edwards) metabolism: implications for estuarine populations. J. Exp. Mar. Bio. Ecol. 176: 167-185.

Jury, S.H., Kinnison, M.T., Howell, W.H., and Watson, W.H. III. (1994b). The behavior of lobsters in response to reduced salinity. J. Exp. Mar. Bio. Ecol. 180: 23-37.

Katz, C.H., Cobb J.S., and Spaulding, M. (1994). Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. Mar. Ecol. Prog. Ser. 103: 265-273.

Lane, E.W., editor (1947) Report of the subcommittee on sedimentary terminology. Trans Amer. Geophys. Union 28: 936-938.

Lavalli, K.L. (1991). Survival of early juvenile American lobsters (*Homarus americanus)* during their first season on diets of mesoplankton, microplankton, and frozen brine shrimp. Fish. Bull. 89: 61-68.

Lavalli, K.L. and Barshaw, D.E. (1986). Burrows protect postlarval lobsters *Homarus americanus* from predation by the non-burrowing cunner *Tautogolabrus adspersus* but not from the burrowing mud crab *Neopanope texani*. Mar. Ecol. Prog. Ser. 32: 13-16.

Lawton, P. and Lavalli, K.L. (1985). Postlarval, juvenile, adolescent, and adult ecology. *In* "Biology of the Lobster *Homarus americanus"* (edited by Factor,J.R.) Academic Press, NY. pp. 47-88.

McLeese, D.W. (1956). Effects of temperature, salinity and oxygen on the survival of the American lobster. Can J. Fish. Res. Board Can. 13: 247-272.

Miller, R.J. (1989). Catchability of American lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) by traps. Can. J. Fish. Aquat. Sci. 46(10): 1652-1657.

Miller, R.J. (1997). Spatial differences in the productivity of American lobster in Nova Scotia. Can. J. Fish. Aquat. Sci. 54(7): 1613–1618.

Miller, R.J. (1985). Seaweeds, sea urchins, and lobsters: A reappraisal. Can. J. Fish. Aquat. Sci. 42(12): 2061-2072.

Nelson, K., Hedgecock, D., and Borgeson, W. (1988). Factors influencing egg extrusion in the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 45(5): 797-804.

Nelson, K., Hedgecock D., and Borgeson, W. 1988. Effects of reproduction upon molting and growth in female American lobsters (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 45(5): 805-821.

Nelson, K. (1986). Photoperiod and reproduction in lobsters (*Homarus*). Amer. Zool. 26: 447-457.

Nelson, K., Hedgecock, D., Heyer, B., and Nunn, T. (1983). On the nature of short-range growth inhibition in juvenile lobsters (*Homarus americanus*). J. Exp. Mar. Bio. Ecol. 72: 83-98.

Ojeda, F.P. and Dearborn, J.H. (1990). Diversity, abundance and spatial distribution of fishes and crustaceans in the rocky subtidal zone of the Gulf of Maine. Fish. Bull. 88(2): 403-410.

Ojeda, F.P. and Dearborn, J.H. (1991). Feeding ecology of benthic mobile predators: Experimental analyses of their influence in rocky subtidal communities of the Gulf of Maine. J. Exp. Mar. Biol. Ecol. 149(1): 13-44.

Pettijohn, F.J. (1949). "Sedimentary Rocks". Harper and Row, NY.

Phillips, B.F. and Sastry, A.N. (1980). Larval ecology. *In* "The Biology and Management of Lobsters,"(J.S. Cobb and B.F. Phillips, eds.) Vol. II. Academic Press, NY. pp.11-57.

Phillips, B.F., Cobb, J.S. and George, R.W. (1980). General Biology *In* "The Biology and Management of Lobsters," (J.S. Cobb and B.F. Phillips, eds.) Vol. I. Academic Press, NY. pp. 1-82

Platt, D.D. (1998). "Rim of the Gulf-Restoring Estuaries in the Gulf of Maine." The Island Institute, Rockland, ME.

Pottle, R.A. and Elner, R.W. (1982). Substrate preference behavior of juvenile American lobster, *Homarus americanus*, in gravel and silt-clay sediments. Can. J. Fish. Aquat. Sci. 39: 928-932.

Roberts, D.C. (1996). "A Field Guide to the Geology of Eastern North America" Houghton Mifflin Co., NY.

Robichaud, D.A. and Campbell, A. (1995). Movement, reproduction and growth of ovigerous lobsters (*Homarus americanus*) from Newfoundland released off Grand Manan, Bay of Fundy. J. Shell. Res. 14(1): 199-204.

Rooney, P. and Cobb, J. S. (1991). Effects of time of day, water temperature, and water velocity on swimming by postlarvae of the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 48(10): 1944-1950.

Scarratt, D.J. and Raine, G.E. 1967. Avoidance of low salinity by newly hatched lobster larvae. J. Fish. Res. Board Can. 24: 1403-1406.

Steneck, R.S. (1989). The ecological ontogeny of lobsters: in situ studies with demographic implications. *In* "Life History of t he American Lobster." Proceedings of a Workshop, Nov 29-30, 1989, Orono, ME. (Kornfield, I. Editor), Lobster Institute, Orono, ME. pp. 30-33.

Steneck, R.S. and Wilson, C. (1998). Why are there so many lobsters in Penobscot Bay? *In* "Rim of the Gulf-Restoring Estuaries in the Gulf of Maine" (edited by Platt, D.D.) The Island Institute, Rockland, ME. pp. 72-75.

Talbot, P. and Helluy, S. (1995). Reproduction and embryonic development *In* "Biology of the Lobster *Homarus americanus"* (edited by Factor, J.R.) Academic Press, NY. pp. 191-201.

Templeman, W. (1937). Egg-laying and hatching postures and habits of the American lobster (*Homarus americanus).* J.Biol. Board Can. 3: 339-342.

Templeman, W. (1936). The influence of temperature, salinity, light, and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Board Can 2: 485-497.

Thomas, M.L.H. and White, G.N. (1969). Mass mortality of estuarine fauna at Bideford, P.E.I., associated with abnormally low salinities. J. Fish. Res. Board Can. 26: 701-704.

Uzmann, J.R., Cooper, R.A., and Pecci, K.J. (1977). Migration and dispersion of tagged American lobsters, Homarus americanus, on the Southern New England continental shelf. NOAA Tech. Rep. NMFS SSRF-705.

Waddy, S.L. and Aiken, D.E. (1990). Intermolt insemination, an alternative mating strategy for the American lobster (*Homarus americanus).* Can. J. Fish. Aquat. Sci. 47: 2402-2406.

Waddy S.L., Aiken, D.E. and De Kleijn, D.P.V. (1995). Control of growth and reproduction in "Biology of the Lobster *Homarus americanus"* (edited by Factor, J.R.) Academic Press, NY. pp. 244-249

Wahle, R.A. (1992). Substratum constraints on body size and the behavioral scope of shelter use in the American lobster. J. Exp. Mar. Biol. Ecol. 159: 59-75

Wahle, R.A.; Steneck, R.S. (1991). Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Mar. Ecol. Prog. Ser. 69: 231-243.

Wahle, R.A. and Steneck, R.S. (1992). Habitat restrictions in early benthic life: Experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. and Ecol. 157: 91-114.

Wahle, R. A. and Steneck, R.S. (1991). Recruitment, substratum selection and the impact of predators on early benthic phase American lobsters, *Homarus americanus*. Mar. Ecol. Prog. Ser. 69: 231-243.

Weiss, H.M. (1970). The Diet and Feeding behavior of the lobsters, *Homarus americanus* in Long Island Sound. PhD dissertation Univ. of CT, Storrs, CT.

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. J. Geol. 30: 377-392.

Wiggin, J. and Mooers, C.N.K., (editors) (1992). Proceedings of the Gulf of Maine Scientific Workshop, Urban Harbors Institute, Univ. of Mass. Boston MA. pp. 51-74.

KEY MAP REFERENCES

Banner, A.H. and Hayes, G. (1996). Identification of important habitats in coastal New Hampshire. (unpublished). Avail. @ http//rossby.unh.edu/edims/banner/gbay

Bigelow, H.B. (1927). Physical oceanography of the Gulf of Maine. Fish. Bull. 40: 511-1027.

Davis, C.W. (1978). Seasonal bottom-water temperature trends in the Gulf of Maine and on Georges Bank, 1963-75. NOAA Tech. Report NMFS SSRF-725,

Fritz, R.L. (1965). "Serial Atlas of the Marine Environment - Folio 10 Autumn Distribution of Groundfish Species in the Gulf of Maine and Adjacent Waters 1955-1961." Amer. Geog. Soc. NY.

Grosslein, M.D. and Azarovitz, T.R. (1982). "Fish Distribution MESA New York Bight Atlas" Monograph 15; Sea Grant Institute, NY.

Holboke, M.J. and Lynch, D.R. (1995). Simulations of the Maine Coastal Current. *In* Proceedings of the ASCE 4th. International Conference on Estuarine and Coastal Modeling, San Diego, CA.

Kelly, J.T. and Dickson, S.M. (1996). Surficial geology of the Maine inner continental shelf. Dept. of Cons. Nat. Res. Info. and Map. Center, Maine Geol. Survey; Maps No 96-1 to 96-7, 1:100,000 scale.

Knebel, H.J. and Circe, R.C. (1995a). Maps and diagrams showing acoustic and textural characteristics and distribution of bottom sedimentary environments, Boston Harbor and Massachusetts Bay. MA., USGS Misc. Field Studies MAP MF-2280, 1:150,000 scale.

Knebel, H.J. and Circe, R.C. (1995b). Sea floor environments within the Boston Harbor- Massachusetts Bay sedimentary system: A regional synthesis. J.Coast. Res. 11(1): 230-251.

Knebel, H.J., Rendigs, R.R., List, J. H., and Signell, R.P. (1996). Sea floor environments in Cape Cod Bay, a large coastal embayment. Mar. Geol. 133: 11-33

NOAA. (1986). Bathymetric fishing map, (Provincetown quad), 1:100,000 scale.

NOAA. (1986). Bathymetric fishing map, (Gloucester quad) 1:100,000 scale.

NOAA. (1987). Bathymetric fishing map (Chatham quad) 1:100,000 scale.

Osberg, P.H., Hussey, A.M., and Boone, G.M. (1985). Bedrock geologic map of Maine, Maine Geol. Survey, 1:500,000 scale.

Patey, S. (1996). "The Coast of New England- A Pictorial Tour From Connecticut to Maine". International Marine, Rockport Publishers Inc, ME.

Poppe, L.J., Schlee, J.S., Butman, B. and Lane, C.M. (1989). Map showing the distribution of surficial sediment - Gulf of Maine and Georges Bank. USGS Misc. Inv. Series MAP I-1986A, 1:1,00,000 scale.

Poppe, L.J., Schlee, J.S. and Knebel, H.J. (1994). Map showing distribution of surficial sediment on the Mid-Atlantic Continental Margin, Cape Cod to Albemarle Sound. USGS Misc. Inv. Series MAP I-1987-D, 1:1,00,000 scale.

Strahler, A.N. (1966). "A Geologist's View of Cape Cod". Natural History Press, MA.

US Dept. of Interior. (1976). Environmental Impact Statement for Lease Sale 42. Min. Mgmt Serv. Wash. D.C.

Thompson, W.B. and Borns, HW., Jr. (1985). Surficial geologic map of Maine: Maine Geological Survey, 1:500,000 scale.

Valentine, P.C., and Lough, G.R. (1991). The sea floor environment and the fishery of Eastern Georges Bank, USGS, NMFS Open-file Report 91-439.

Valentine, P.C., Strom, E.W. Lough, G.R., and Brown, C.L. (1993). Maps showing the sedimentary environment of Eastern Georges Bank. USGS, NMFS, Misc. Inv. Series, MAP I-2279-B, 1:250,000 scale.

Valentine, P.C., Schmuck, E.A. Signell, R.P. and Ryland, C.A. (1995). Sea floor topography of Massachusetts and Cape Cod Bays and Stellwagen Bank Nat'l Marine Fisheries Sanctuary. USGS Open File Report 95-7