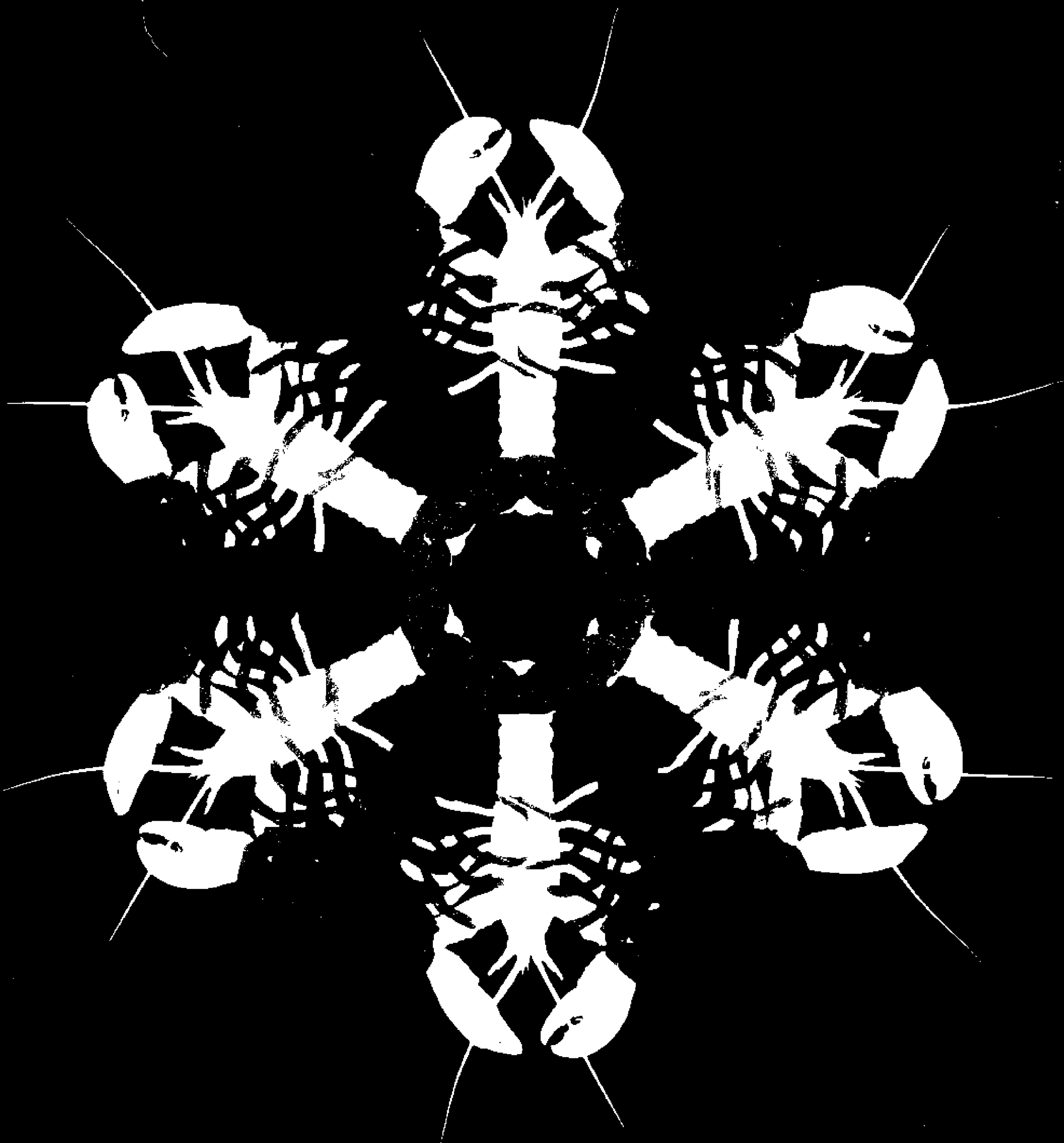
The American Lobster: The Biology of *Homarus americanus*



The American Lobster: The Biology of *Homarus americanus*

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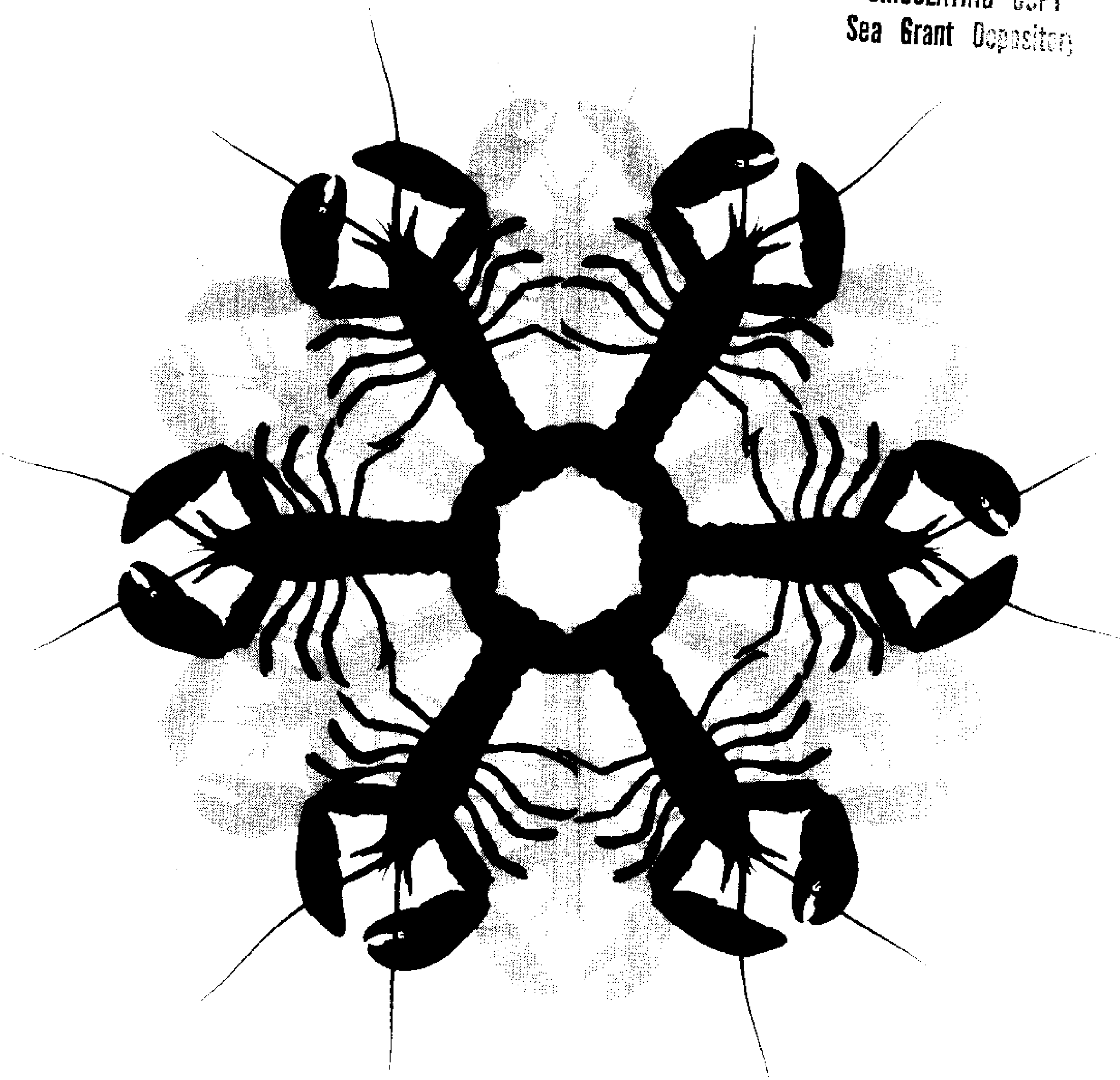

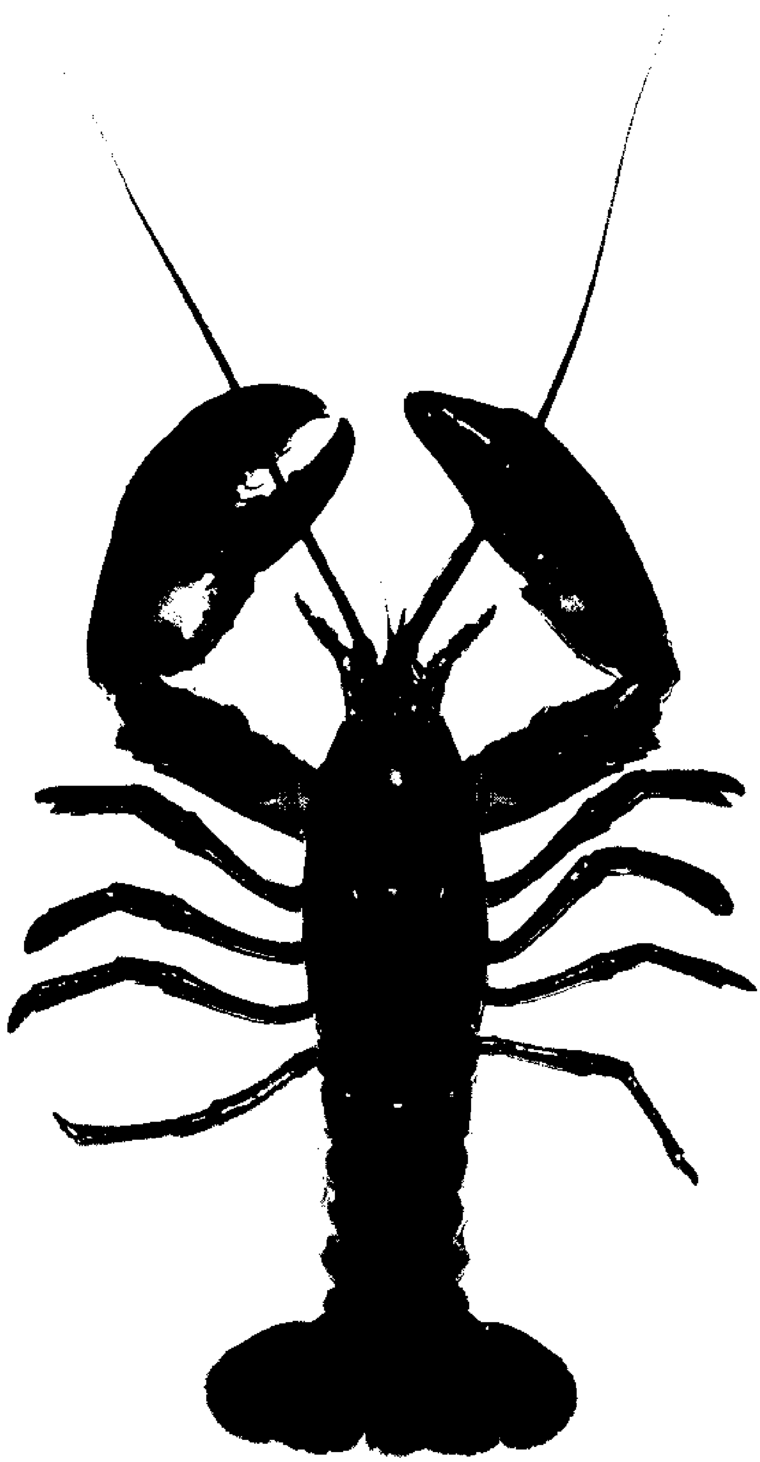

Contents

Introduction

The American lobster, *Homarus americanus* Milne-Edwards, is an animal of considerable interest to a large number of people for a wide variety of reasons. Most people are familiar with the general appearance of *Homarus americanus*, both alive and boiled, but few know very much more. To many, there is a mystique surrounding the purchase, cooking, and eating of lobster that is unrivaled by other foods. To others, the lobster represents a source of income: The commercial lobster fishery along the northeast coast of the U.S. is one of the most heavily exploited and valuable. To some researchers, the lobster represents a valuable experimental marine animal because a good deal is known about its anatomy and physiology. Recently, some people have become interested in the possibility of commercial lobster aquaculture.

This booklet has been written with the goal of communicating some basic information concerning the lobster's biology, behavior, and value to man. It is not meant to be a complete review of the scientific literature regarding lobsters, but it gives those interested in pursuing the subject a starting point from which to conduct their own review. To this end, the bibliography, although far from complete (a recent exhaustive bibliography (113) on *Homarus* contained over 3000 entries), lists a number of papers not referred to in the text. Citation of a reference is done by placing the reference number in parentheses. The serious student of the lobster will want to read many of these papers, perhaps starting with Herrick's magnificent monograph on the natural history of *Homarus americanus* (65). A good report on lobster biology and the New England fishery for lobsters is found in E.L. Doliber's book (35a). For younger readers, I recommend Herb Taylor's beautifully illustrated "The Lobster: Its Life Cycle" (164a). The booklet you are now reading is designed to give the reader a feel for the great deal of information available on the lobster, to specify those areas of study worthy of continued research, and to promote an appreciation for the lobster as a living animal with due regard to its importance for man.

Acknowledgments

Many people have helped in the preparation of this booklet. Robert Anderson did the early literature search and organization. Marcia Grey continued with the literature search, editing, and typing. The research assistance of George Tamm allowed me to spend more time writing than would otherwise have been possible. Several people critically read the manuscript at various stages: Lynne Zeitlin-Hale, Hal Goodwin, Dick Ford, George Tamm, and John Hughes. Sara Callaghan gave editorial assistance. Dick Wilder, Don McLeese, Paul Chapman, Jim Carlberg, Akella Sastry, and Herb Taylor supplied material for some of the illustrations. Bob Dano did most of the line drawings. Many graduate students assisted along the way. To everyone who helped: Many thanks!

Illustration Credits:

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The Lobster: Its Life Cycle
Sterling Publishing Co., Inc., N.Y. 1975
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Figure 7, from Herrick 1911, *The Natural History of the American Lobster* (65).
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General Biology

Taxonomic Position. *Homarus americanus* is a crustacean of the order decapoda, sub-order reptancia, section macrura, all of which means that it has ten legs, crawls rather than swims, and is shrimp-like rather than crab-like in form.

Anatomy. The body of the lobster is composed of 21 segments. All but the terminal segment carry paired, jointed appendages. The anterior section (cephalothorax), which is covered by the single-pieced shell or carapace, contains the first 14 segments. The lobster has five pairs of walking legs (pereiopods) but appears to have only four, as the first pair have been modified to form the large crusher and ripper claws. Of the walking legs, the first two pairs have small pincers or chelae, while the last two pairs simply taper to a point. The last seven segments form the abdomen. Under the abdomen are six pairs of swimmerets (pleopods); the terminal pair are enlarged into uropods and make up the tail fan on either side of the telson (Figure 1).

Sexual differences are exhibited in the first pair of pleopods. In males, these are rigid structures which, when placed together, form an intromittent organ used to convey sperm to the female. The male has paired testes, each connected by a coiled duct (the vas deferens) to the base of the last walking leg. The sperm are carried down the vas deferens and ejaculated embedded in a gelatinous mass, the spermatopore. When turned on her back, the female displays a blue shield between the bases of the last two walking legs. This is the seminal receptacle, which receives and stores sperm. Just anterior to the sperm receptacle are the paired openings of the oviducts, which carry eggs from the ovaries out of the body. The ovaries lie dorsally in the cephalothorax and in the first few segments of the abdomen. In females, the first pair of pleopods are very small but otherwise similar to the others.

Other distinctions between mature male and female lobsters are noticeable on the abdomen. The female's abdomen is about as wide as the carapace, while the male's is somewhat narrower. The male has sharp spines under the abdomen, while the female's spines are blunt.

The characteristic greenish-brown color of the adult is due primarily to the presence of pigments in the chromoplasts, which lie beneath the cuticular epithelium. A blue, red, or mottled appearance may have a genetic basis. The red color of the cooked lobster results when heat denatures the masking green pigment.

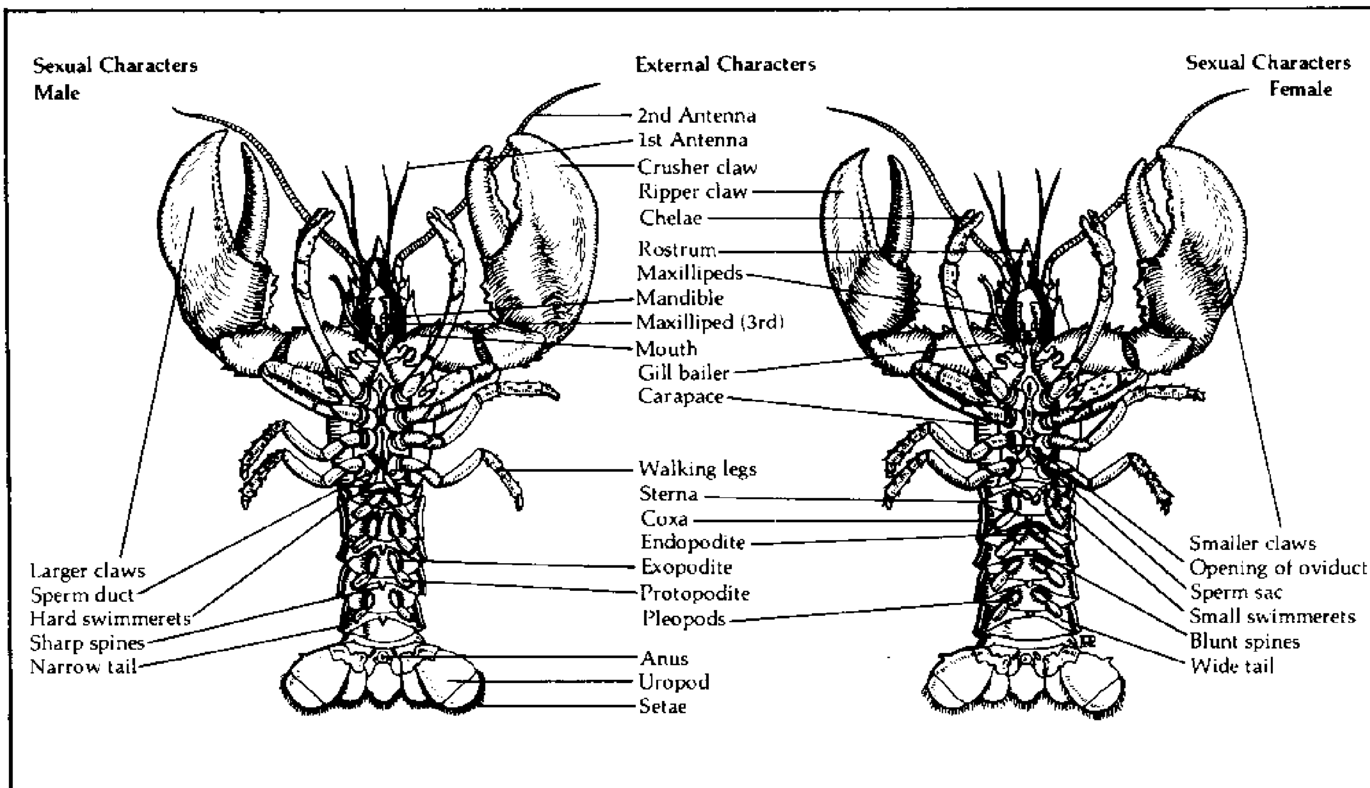


Figure 1. External anatomy of the lobster from the ventral surface. *Left:* Male. *Right:* Female.

Nervous System and Sense Organs. The nervous system of *Homarus* is typical of decapods in general. The "brain," or supra-esophageal ganglion, is a large mass of nerve cell bodies (ganglion) lying between the eyes and above the esophagus or throat. It receives nerve fibers from the eyes and first and second antennae. This ganglion is connected to the central, chain-like nerve cord that runs the length of the body and includes other ganglia (Figure 2). The brain is the only major ganglion in the dorsal half of the body; all others are ventral. The most anterior of these ganglia is the subesopheageal, lying just below the mouth and innervating the mouth parts. Thoraic and abdominal ganglia in series innervate the body wall and appendages.

The compound eyes of the lobster are borne on movable stalks. The eye is composed of approximately 14,000 simple lens-retina units called ommatidia. When magnified and viewed from above, they give the eye a mosaic appearance. Each ommatidium has pigment cells which, when moved away from the body, allow adaptation to bright light by screening the sides of the ommatidium so that light cannot pass from one ommatidium to the next. Image perception is presumed possible; although images may not be distinct, movement is easily detected. It is not known whether lobsters can distinguish colors as can other crustaceans. Their spectral sensitivity ranges from 400-600 nanometers (nm), with a peak sensitivity in the green range at about 520 nm (78). In the larval stages, a median ocellus (single, light-sensitive structure) is located near the brain. The last ganglion of the abdomen is also thought to be light sensitive (15).

Both mechanical and chemical stimulation influence the lobster's behavior. The second (longer) antennae, claws, and walking legs are liberally supplied with tactile hairs. These are important for maintaining contact with the environment.

The minute hair peg and hair fan organs found on the anterior portion of the carapace and on the claws are sensitive to water movements and low-frequency vibration (83, 84, 86). Statocysts, equilibrium receptors comparable in function to the vertebrate semicircular canals, are located on the basal joint of the first antennae (Figure 3). These detect the animal's position relative to gravity and

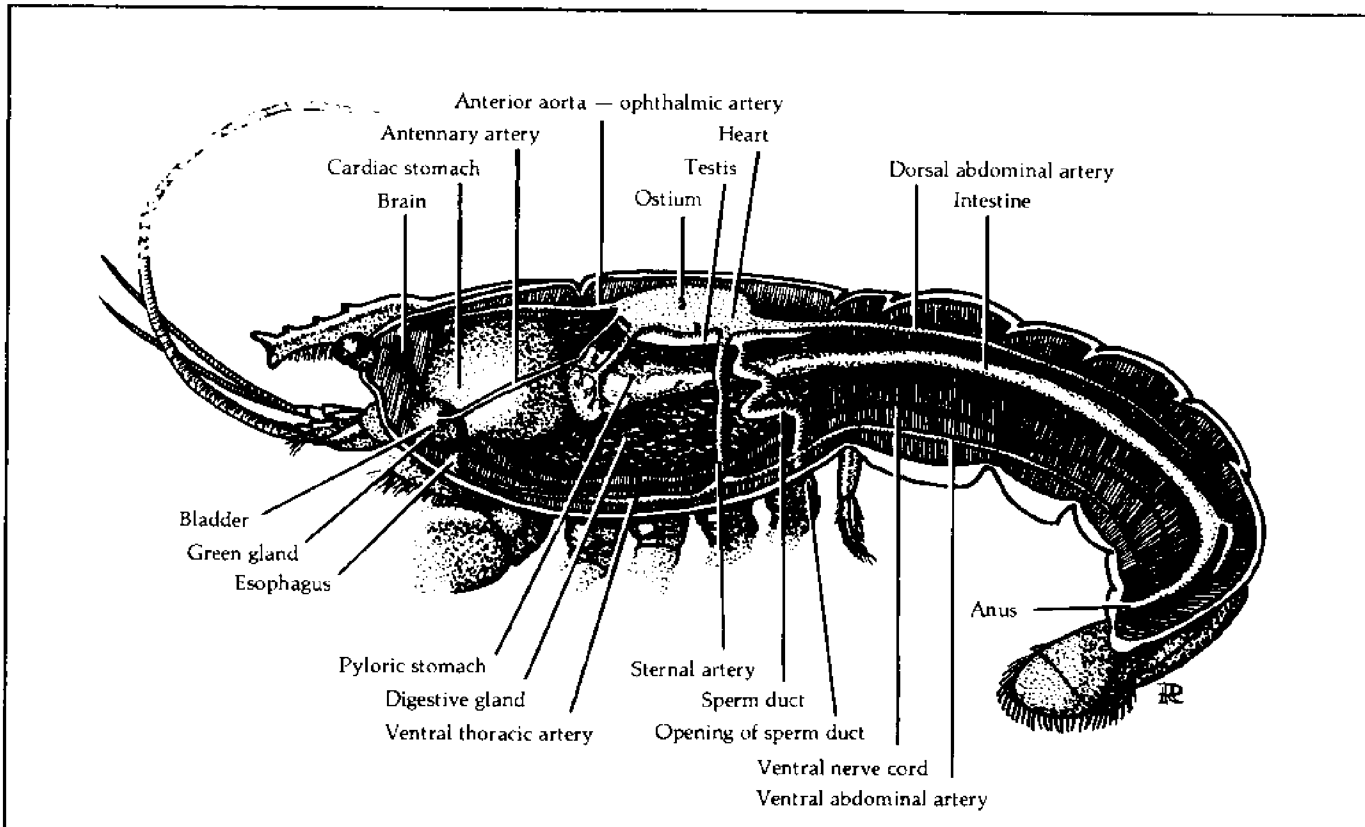


Figure 2. Internal anatomy of the lobster.

are also sensitive to rotation, acceleration, and deceleration (26, 27).

Lobsters are sensitive to a wide range of chemical substances, which are perceived by receptors located on the claws, the walking legs, the mouth parts, and the antennules or first antennae (142). Lobsters will walk upstream toward odor sources such as food extracts, amino acids, or other chemical compounds (98, 100-104). However, they are not particularly responsive to water in which live prey, such as sea urchins, mussels, clams, and crabs, have been kept (103). The lateral branch of antennules are particularly sensitive to amino acids and are presumably the organs used in reception of distant chemical stimuli (1, 143). The medial branch may serve the function of orientation to water current (103).

Respiration and Circulation. The elongated, feathery gills are found in cavities on either side of the body, arching upward from the bases of the legs (Figure 4). Water currents set up by rhythmic movements of the gill "bailers," one of the mouthpart appendages called second maxillae, enter the posterior end of the gill cavity and exit through the anterior end near the mouth parts. Lobsters held out of water for some time appear to "froth at the mouth." These bubbles are caused by air being moved through the damp gill-cavity passages.

The circulatory system consists of a heart, arteries and veins, and a system of irregular channels called sinuses (Figures 2, 4). The slightly bluish blood of the lobster carries the respiratory pigment hemocyanin.

Digestive System. Food, torn apart but not completely chewed by the mouth parts, enters the esophagus, travels to the anterior or cardiac stomach, and hence to the gastric mill, which is lined with calcareous toothed slates and where the food is ground (Figure 2). The fine particles then enter the posterior or pyloric division of the stomach where they are strained, sorted, and acted upon by digestive enzymes secreted by the hepatopancreas. Larger, undigested particles enter the hind gut — a simple, straight tube — and are eliminated through the anus at the base of the tail.

Nitrogenous wastes, largely ammonia, are excreted by the gills and by the antennal glands in the anterior ventral

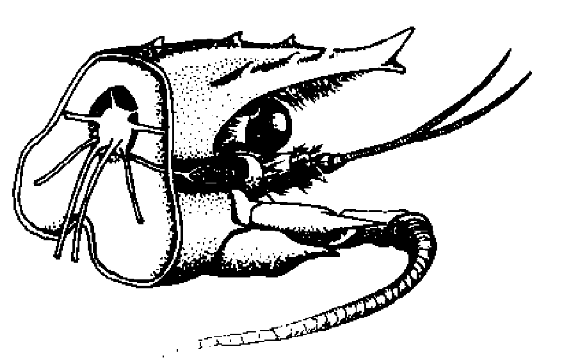


Figure 3. Cutaway drawing of head region showing the location of the statocyst at the base of the first antenna. Redrawn from Cohen (26).

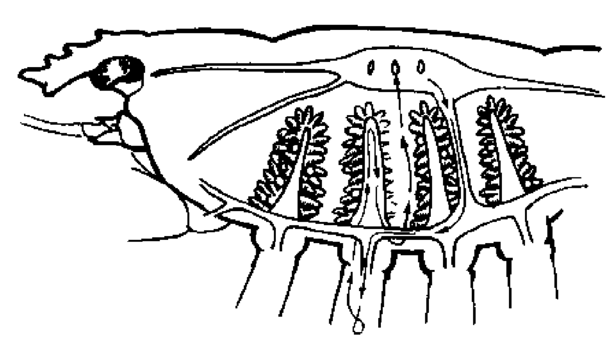


Figure 4. Diagrammatic representation of gills and circulatory system. Arrows show the direction of blood flow.

Figure 5. Egg laying posture.

Figure 6. Egg hatching posture.

part of the body through a pore on the lower side of the basal segment of the first antennae. Occasionally, when a lobster is picked out of the water, a fine spray of water may be seen coming from this area; this is the urine of the lobster.

Life Cycle. Mating occurs only when the female is soft after molting. The sperm may be stored in the seminal receptacle for as long as 15 months until the eggs are laid. The eggs stream from the oviducts, pass over the sperm receptacle where they are fertilized, and are then cemented to the swimmerets. During this process, the female lies on her back with the tail curled to form a pocket which catches the eggs flowing down from the oviduct (Figure 5). The female is then said to be "in berry," which usually occurs once every other year. She carries the eggs 10 to 11 months before hatching, the number of eggs varying with her size. When maturity — 75 to 88 mm. carapace length — is reached, about 7000 eggs are laid. A female at maximum size may carry up to 80,000 eggs at one time (126). During embryonic development the eggs swell, evidently from water absorption across the embryo surface. The water content of the embryo increases from 56.2 percent to 86.8 percent, while the energy content decreases from 6,636 to 4,292 cal./g. dry wgt. The freshly hatched larva utilizes as much as 60.3 percent of the energy contained in the egg (116). At the time of hatching, the internal pressure thus generated bursts the outer egg membrane, which sloughs off completely but remains attached at the cephalic end of the egg to the inner membrane and eggstalk. The inner membrane tears because of the egg weight and swimmeret action. The liberation of the larva from the egg is also accomplished by this swimmeret action. The emerging lobster larva is still in an immobile stage. The newly hatched larva molts immediately or within a short time, and the first pelagic stage swims freely (33).

In Massachusetts, hatching begins about mid-May,

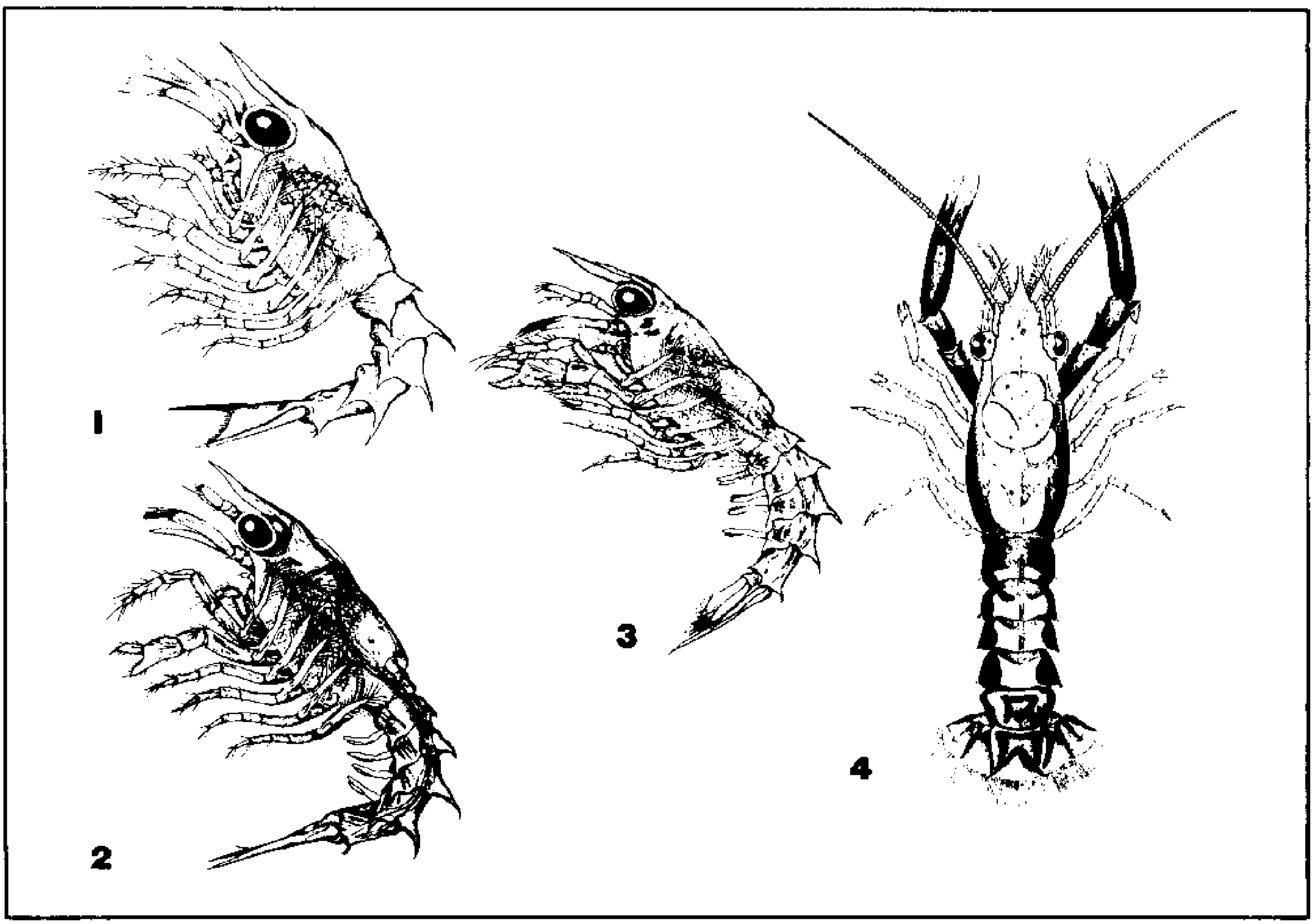


Figure 7. The four larval (free swimming) stages.

when water temperatures rise to approximately 15° C (70). The female assumes a tail-up posture, standing on the tips of her walking legs, and waves her swimmerets to release several hundred larvae at a time (Figure 6). Hatching generally occurs shortly after it becomes dark (45).

Lobster larvae molt four times. First, second, and third stage larvae look different and behave differently from the adult. They are free-swimming for the first three stages, which last 10 to 20 days depending on water temperature (70). After molting into the fourth stage, the larva resembles the adult, yet continues to swim for several days before becoming bottom seeking. Fifth-stage lobsters are probably completely bottom-seeking, although swimming is often seen (Figure 7).

From first stage larva to maturity, the lobster molts 20 to 25 times, with ten or so of these molts occurring in the first year of life. The increase in size at each molt ranges from ten percent to 17 percent and is about 50 percent in weight (Figure 8.)

In nature, there are usually two peaks of molting: early spring and early fall. After the early years, there are two to four molts per year until about age five, after which the average lobster molts annually. Larger lobsters molt less frequently, probably once every several years. In the commercial fishery, "legal" size is reached after five to seven growing seasons, depending upon water temperature. Having reached sexual maturity, females molt and carry eggs in alternate years. Since the eggs are carried for many months, there is no opportunity for molt to occur during this time. Thus the molting frequency of the mature female is effectively one half that of the male.

The growth rate is also influenced by water temperature. By increasing the temperature in the laboratory, lobsters can be made to grow considerably faster (72).

Water temperature is also a major factor in embryonic development. The time from egg extrusion to hatching is 39 weeks at a constant 10° C, and 16 weeks at 20° C. There appears to be no difference in egg development rate

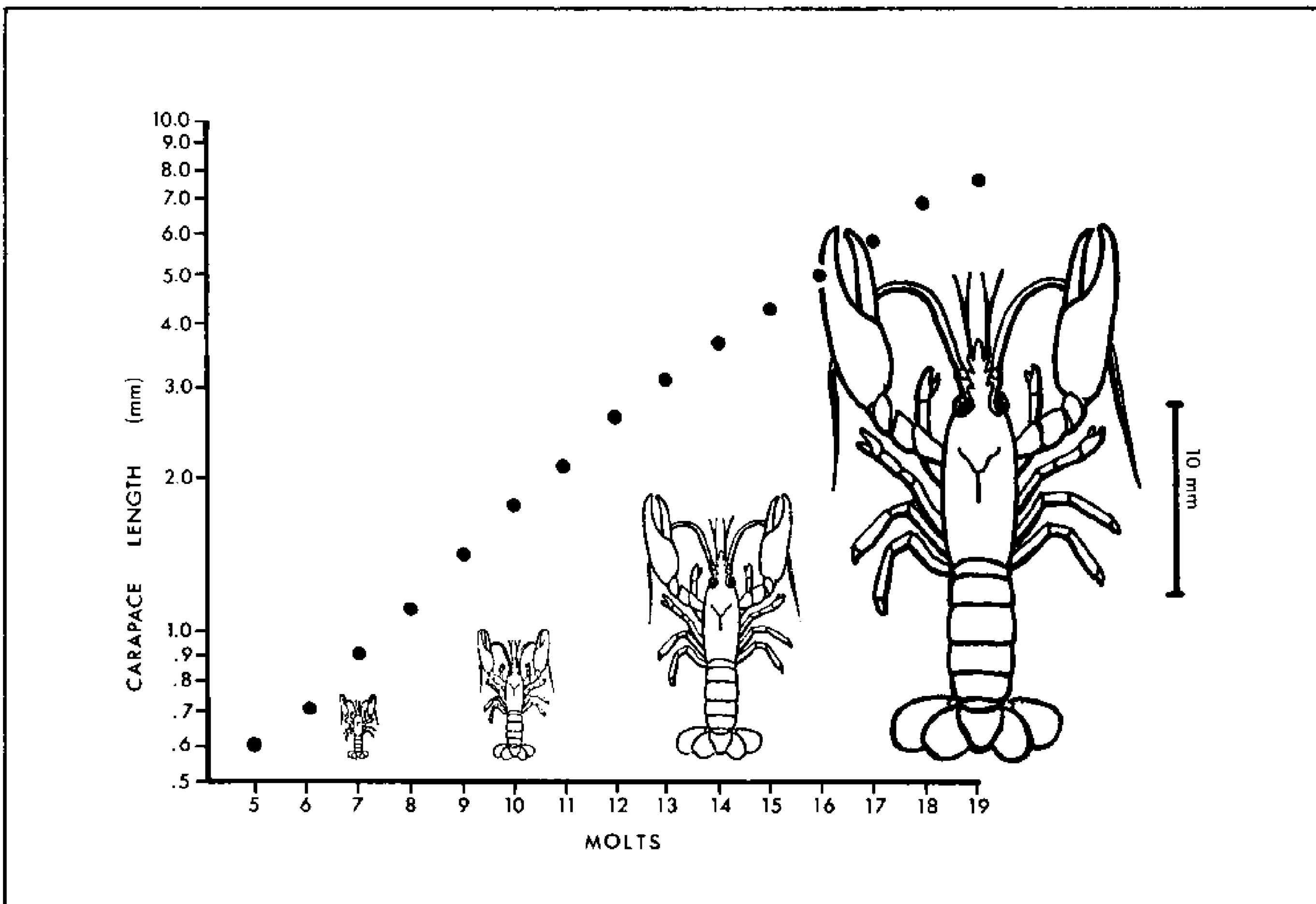
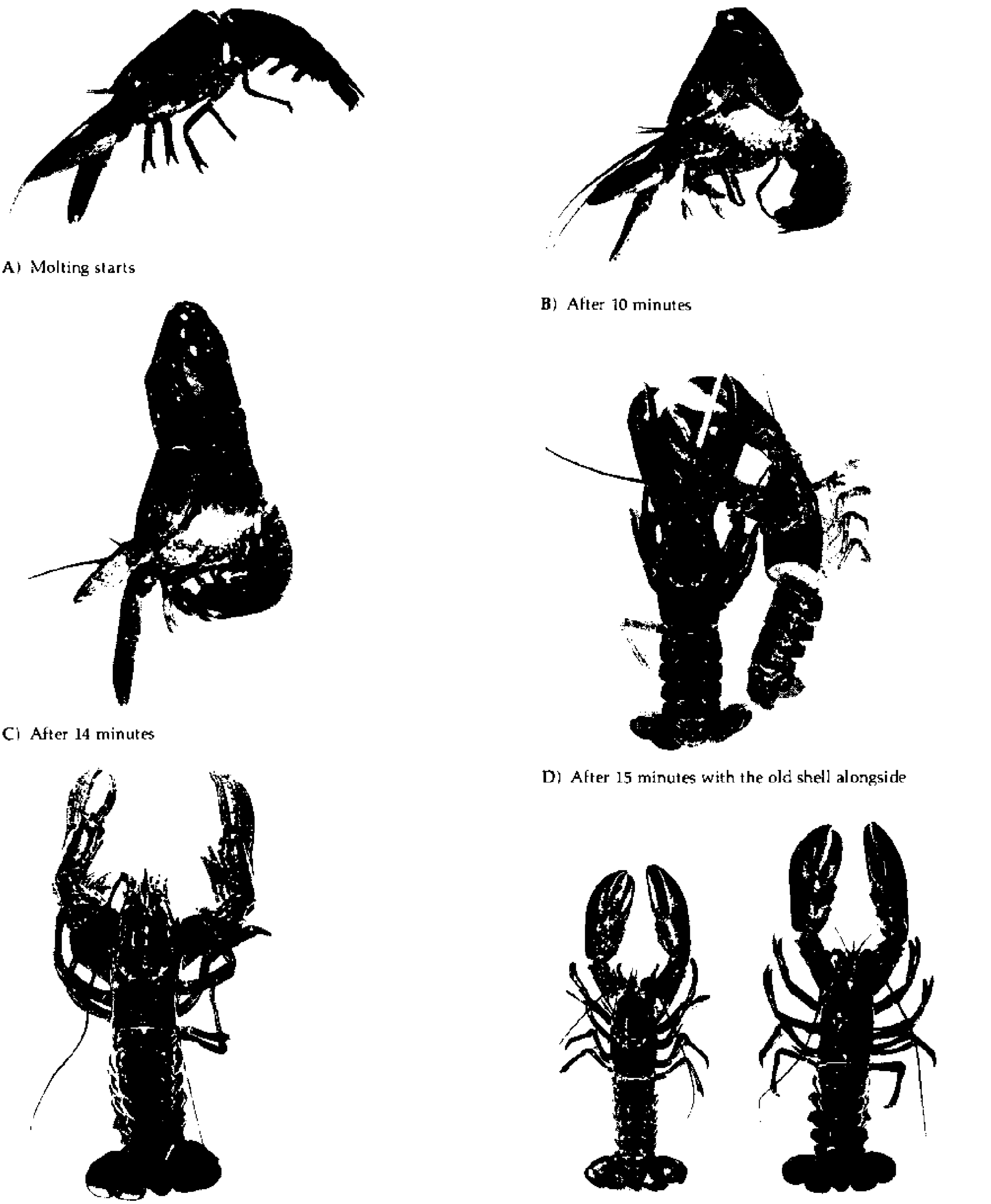


Figure 8. Increase in size with each molt.



A) Molting starts

B) After 10 minutes

C) After 14 minutes

D) After 15 minutes with the old shell alongside

E) After 15 minutes.
Notice the claws are not yet filled out.

F) After 5 hours. Old shell on left;
newly molted lobster on right has swollen to full size.

Figure 9. The molting process.

whether the temperature fluctuates around a mean temperature — as in the natural environment — or is held constant (119).

Molting. Although growth occurs during most of the period between molts, an increase in size can occur only through molting (ecdysis). A lobster approaching ecdysis can be distinguished by the dull red color of the old shell, a reddish-brown color of the membranes, particularly under the abdomen, and the development of new setae in the pleopods (3).

The molting process is typical of that for most crustaceans (117). At the time of ecdysis, the dorsal membrane between the carapace and the abdomen splits. The lobster rolls over on its side, bends into a V-shape, and starts to withdraw from the shell (Figure 9). At this point, the carapace will often split longitudinally along the dorsal midline. The muscles become relaxed, and body fluids are drawn from the extremities, causing them to shrink. This shrinkage is considerable, since the size of the claws must be reduced by approximately one-fourth of their normal size to be withdrawn through the narrow segment at the base of the claws. Once out of the old shell, body fluids return to the extremities and water is absorbed. Over a period of several hours, the lobster swells to a size considerably larger than that of its old shell. Hardening of the shell takes a variable length of time, dependent on such factors as food, water temperature, and the age of the lobster.

Molt-inhibiting hormones, which are produced in the neurosecretory centers of the eyestalk, prohibit the induction of premolt conditions. Removal of the eyestalks induces faster molting (52, 120, 149) by allowing molt-promoting hormones (including ecdysterone, the so-called "molting hormone") to become effective. Ecdysterone probably does not induce all premolt conditions, but mediates the formation of new cuticle. In addition, the reported "Y" organ of crustacea, which also supposedly controls molting, apparently is not present in lobsters (148, 150).

Autotomy and Regeneration. Like other crustacea, lobsters can reflexively amputate (autotomize) any of the chelae and walking legs. When grasped by the claws, as when a diver attempts to remove it from a burrow, the lobster can release the claw. The fracture occurs on the "breaking plane" at the second basal joint. Autotomy can be induced by crushing the appendage or by stimulating the nerve of the limb. Upon autotomy, the blood flow through the arteries to the limb is shut off.

Appendages lost by autotomy or injury can be regenerated. A limb bud forms at the point where the appendage was lost (Figure 10). At the next molt, the entire appendage appears fully formed, but smaller in the case of the claws. Regeneration may either increase or decrease the time between molts, depending on when the injury occurred and the age of the lobster (43, 177). A lobster in the process of regenerating a limb will not increase in size at molt as much as an intact animal, but after three molts it will be as large as a lobster that had not lost a claw (70).

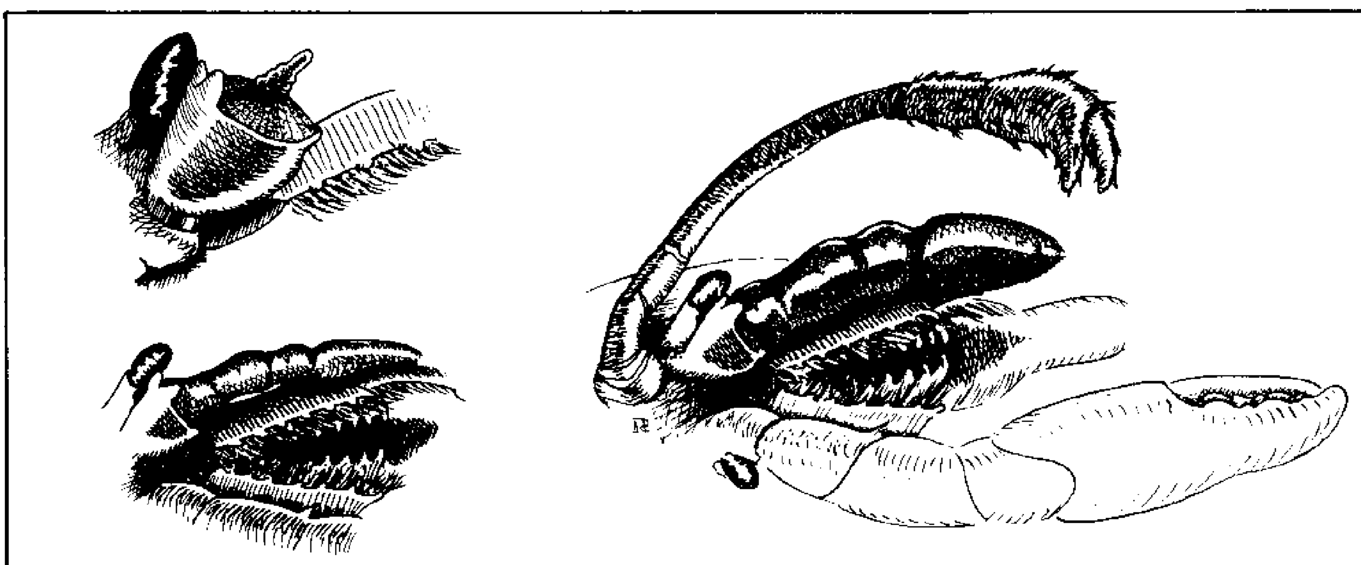


Figure 10. Steps in regenerating a lost claw. *Left Above:* Base of the large claw showing the breaking plane and the formation of a small limb bud. *Left Below:* Enlargement of the limb bud. *Right:* Limb bud just prior to molting. The claw on the other side has been drawn in (not to scale) for reference. Redrawn from Goss (59a).

Ecology and Behavior

Ecology

Adult Distribution. The lobster is found along a 7,000-mile stretch of North America, inshore from the Straits of Belle Isle, Newfoundland, to Virginia, and offshore from Georges Bank to North Carolina. It inhabits depths ranging from one meter to 700 meters, depending on latitude. Lobsters from offshore areas appear to be morphologically distinct from those found inshore (125). Genetic analysis indicates that lobsters are probably separated into breeding or local populations, and that the offshore population may be distinct from the inshore (10, 169).

Larval Ecology. Lobster larvae are generally caught in plankton nets towed on or near the surface during the months of May, June, and July off southern New England, and in July and August in northern New England and Canada. Little is known about their feeding habits, but in laboratory situations, they survive well on chopped mussel or live, brine shrimp nauplii. It is assumed that they are carnivorous and eat smaller zooplankton. Their predators are numerous, probably including virtually all the larger plankton-feeding fishes and possibly comb jellies (ctenophores).

Mortality in larval stages one to four has been estimated at from 50 percent to nearly 100 percent (132, 90). Since there is a possibility the samples do not represent the population, these mortality estimates must be viewed with caution. There is little doubt, however, that few lobsters survive the first 30 days of life.

The abundance of larvae in the surface waters varies greatly. A Canadian study showed a slight relationship between the number of fourth-stage larvae caught and the estimated adult stock available to the fishery five or six years later. There was no relationship, however, between production of larval stages one to three and subsequent stock (129, 132). Essentially, this means it is difficult to predict the number of adult lobsters resulting from any year's larval production. The large variation in larval abundance from year to year may be caused by patchy distribution, which is not revealed by the sampling scheme. It often seems that not enough lobster larvae are found to explain the size of the adult population in an area.

In extensive sampling of the offshore waters of southern New England, very few larvae were caught, although they were distributed fairly evenly in the surface water out to the edge of the Continental Shelf through July and August. Sampling in Long Island and Fisher Island sounds showed a denser concentration in the western end of Long Island Sound (90).

The depth at which larvae swim appears to be regulated by two factors, light and water pressure. Lobster larvae are attracted to dull light but may be repelled by bright light (62). This lasts until about halfway through their fourth stage, at which time they become negatively phototactic. The largest catches of second and third stage larvae are made at the surface on cloudy or rainy days (166). Larvae also seem to be attracted to bright lights hung overboard at night (19).

Pressure sensitivity has been demonstrated by both American and European lobster larvae. All four stages respond to decreased pressure (the equivalent of moving upward in the water column) by swimming downward, and to increased pressure by swimming upward. Larvae in the first three stages, when released at the surface, moved downward. When released at depths of 10, 20, and 30 feet, they moved upward. Stage five, or first juvenile lobsters, did not respond at all to pressure changes (46, 48). It is during the fourth larval stage that the larvae become epibenthic, probably exploring various substrata as well as spending part of their time in the pelagic zone. On the other hand, stage five lobsters settle to the bottom and probably have no need for a depth regulating mechanism.

Lobsters as Predators. The stomach contents of lobsters from the Woods Hole area has been analyzed and found to contain, in decreasing order according to quantity, fish, crustacea (chiefly isopods and decapods), mollusks (mostly small gastropods), algae, echinoderms, and hydroids (65). In Long Island Sound, 90 percent of the lobsters studied had rock crabs, *Cancer irroratus,* in their stomachs (174). Gastropod mollusks were found in 55 percent of the stomachs, bivalves in 55 percent, polychaetes in 59 percent, fish in 49 percent, and plant material in 35 percent. There is no evidence to support the idea that lobsters are primarily scavengers.

Variations in the type of food ingested during the molt cycle were noted. Just after molting, a high proportion of crustacean and mollusk shells — probably a source of calcium — is ingested; just before molting, lobsters tend not to feed. A high proportion of empty stomachs were found in late proecdysis (174).

In Canada, lobsters have been reported to eat sea urchins; a variable but relatively high percentage of stomachs contained sea urchin remains (47, 152, 91, 111, 67). Lobsters may control the sea urchin population by predation, while the herbiverous urchins, in turn, control the size of the kelp *(Laminaria)* population. If lobsters are removed from an area (e.g., by overfishing), the number of sea urchins may increase greatly and the kelp may disappear (91).

There is considerable evidence that the contents of a lobster's stomach reflects the relative abundance of prey species in the habitat. If sea urchins are plentiful, they are eaten; if polychaetes predominate, they may form the major portion of the diet of lobsters in that specific locality.

An energy flow diagram for a seaweed-lobster community in eastern Canada indicates that the lobster consumes slightly less than ten percent of the secondary production of that community (Figure 11) (111).

Lobsters as Prey. Little is known about predators. Many bottom-feeding fishes, such as cod, dogfish, skate, pollock, striped bass, and tautog, probably prey on small lobsters. Codfish are particularly voracious as lobster predators. Large, hardshell lobsters are probably immune to predation (177, 65).

Man is obviously the most important lobster predator. And his activities are not limited to commercial lobster fishing. Irish moss, a commercially important seaweed, is harvested by raking from boats; a Canadian study (133) has shown that up to 5.2 percent of the lobsters in the path of the rake are killed. As many as 280 small lobsters may be killed per boat per day, with many more losing claws or being wounded.

Effects of Environmental Factors

Temperature. Lobsters can withstand a wide range of water temperatures and relatively large thermal shocks. They can survive in water cooled to the freezing point or heated to 32° C (Figure 12). Lethal water temperature levels are not determined by the size of the lobster, and are not affected by a two-month period of starvation (95). As is the case with all cold-blooded animals, however, temperature affects not only survival but also the rate of metabolic functions. Thus, temperature limits the geographical distribution of lobsters and determines the amount of activity lobsters exhibit. Since the walking rate increases with rising temperatures, it would seem reasonable that the colder the water, the less likely lobsters are to encounter pots (Figure 13). The ability to acclimate is cyclical: A lobster approaching molt is less resistant to an increase in temperature than is the intermolt lobster, and is unable to adapt to temperature changes by metabolic alterations (94).

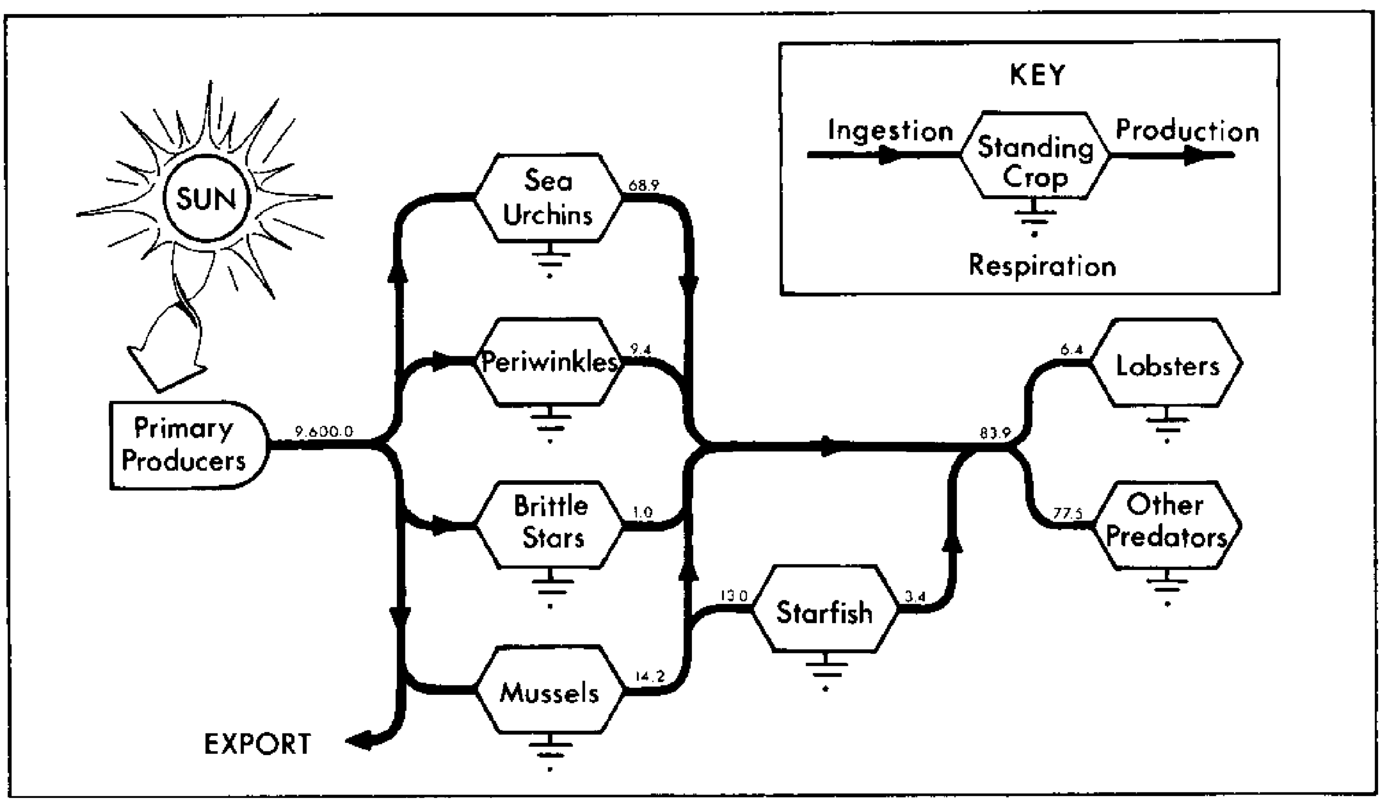


Figure 11. The flow of energy from the sun through plants and herbivores to lobsters and other predators. Values are in kilocalories. Redrawn from Miller et. al. (111).

Salinity. Salinity as low as about eight parts per thousand is the lower limit of tolerance for juvenile and adult lobsters when all other conditions are optimal. There is substantial physiological acclimation to lowered salinity within a period of one week. As with resistance to rising temperature, resistance to lowered salinity is not as great in lobsters approaching molt as in intermolt animals (95). Larvae can tolerate salinities as low as 13.8 parts per thousand but appear to avoid salinities below 21 parts per thousand. This may explain their low numbers near river mouths (135). Lobsters have limited osmoregulatory abilities when the osmotic concentration of the surrounding water is either above or below that of their blood. Excess salt is excreted by the gut, while excess water is excreted by the antennal glands (32).

Oxygen. In studies of oxygen consumption and tolerance, it has been shown that, when other conditions are optimal, lobsters can survive oxygen levels as low as about 1 mg. O_2 per liter (Figure 12). The amount of oxygen consumed per gram of body weight decreases with increasing body weights, and increases with increasing water temperature. As the concentration of oxygen in the water increases, the consumption rate increases. Oxygen consumption is also increased by feeding, crowding, and increased activity (95, 96, 107).

Combined Effects. Temperature, salinity, and oxygen each has certain limits which are lethal when other conditions are optimal. When more than one of these factors is less than optimal, they can combine to produce lethal effects. Figure 12 is a three-dimensional plot of the lethal and tolerance zones at various combinations of temperature, salinity, and oxygen. Using this graph one can determine if a particular set of values is likely to be lethal to a lobster (95).

Pollutants. Many of the chemicals that are toxic to insects are also toxic to lobsters, including pesticides and insecticides. Metals such as copper, Monel, zinc, and lead are lethal at relatively low concentrations (64, 175). Crude oil in very low concentrations slows the lobster's response to food, although the morphology of the chemosensory receptors on the antennules is not altered. It is thought that small quantities of crude oil mixed with seawater produce a noxious smell that may depress the lobster's appetite or chemical excitability (8). The diluted effluent from kraft paper mills does not affect either the behavior of adult lobsters (97, 102) or the survival of larvae and adults (151) at concentrations above those expected in the lobster's natural habitat.

Behavior

Communication. Lobsters communicate with one another by tactile, visual, chemical, and possibly sonic means. The communications are employed during aggressive, sexual, and various other types of encounters.

Male lobsters respond to water in which newly molted

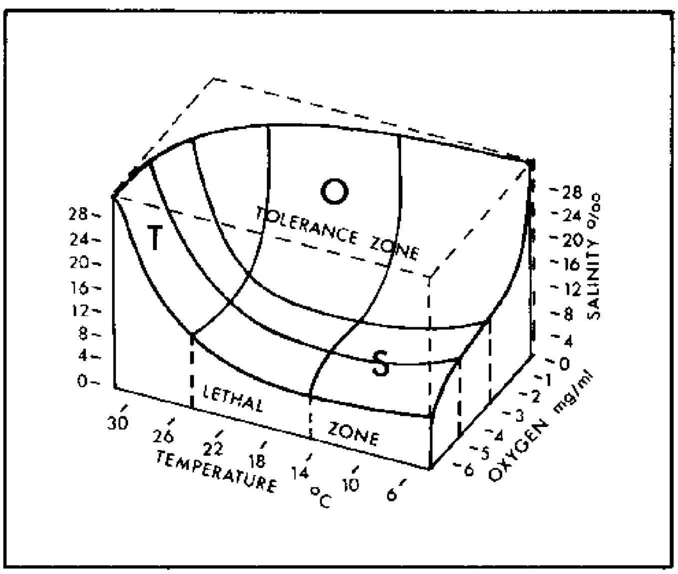


Figure 12. Three-dimensional graph of the tolerance of lobsters to oxygen, salinity, and temperature. Any point in the graph represents a specific combination of oxygen, temperature, and salinity. Redrawn from McLeese (95).

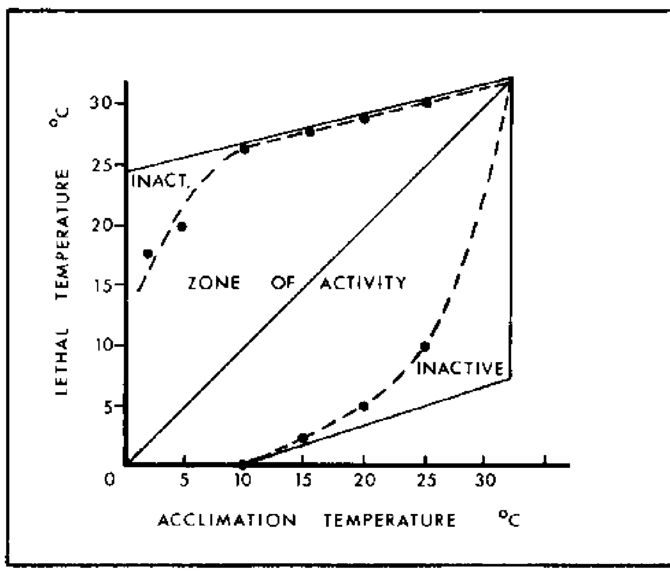


Figure 13. The effect of sudden changes in temperature on the activity of lobsters. Redrawn from McLeese and Wilder (108).

females have been kept (70). The female releases a sex pheromone, a chemical used for communication, which acts like an attractant and stimulates mating behavior in the male. Lobsters will also respond to water from tanks holding other lobsters, except females in the intermolt (hardshell) stage (6, 98, 100, 101). There may be general chemical communications between lobsters that is mediated by more than one pheromone. A sex pheromone has been found in several species of decapod crustaceans. It has been hypothesized that the substance acting as the pheromone is crustecdysone, a crustacean molting hormone (80). There is no evidence that the group of chemicals known as ecdysones or the metabolic products of crustecdysone affect the male lobster's sexual behavior, even though they may be detected in the water (7, 56).

Body and claw size are important visual signals used by lobsters to determine whether a test of strength should be engaged in. The visual communication of lobsters is not complex or elaborate when compared with that of other decapods living in more brightly lit environments. The relative darkness of coastal waters and the lobster's nocturnal nature indicate that visual communication may be less effective than tactile communication.

Lobsters produce low growl-like sounds with a fundamental frequency of 100 to 130 cycles per second (c.p.s.) and a duration of 0.1 to 0.5 seconds (49). These sounds are produced internally by the lateral adductor muscle of the second antennae (110). Lobsters also respond to sounds of similarly low frequency, with a maximum sensitivity between 40 and 75 c.p.s. (114). The sound is apparently produced only when the animal is physically disturbed. It may indicate a mode of communication, but the behavioral significance is unknown.

Activity. Lobsters are active nocturnally. Laboratory studies show that walking increases during the dark period of the light-dark cycle. It is greatest just after the lights go out, then decreases and continues at a somewhat lower level through the dark period (21, 81, 181). Constant bright light over a two-week period suppresses locomotor activity almost completely; constant darkness over a two-week period causes a gradual decrease in activity (21). Communally held lobsters show a higher level of activity than those held individually (181).

Shelter-Related Behavior. During times of inactivity, lobsters are found in burrows under rocks; infrequently, they are found in mud tunnels (168). The youngest juveniles appear well-adapted to living on mud just after the larval stages. In aquaria with mud substrate, they dig U-shaped tunnels by a combination of plowing and pleopod fanning. The mud must be firm enough to support a tun-

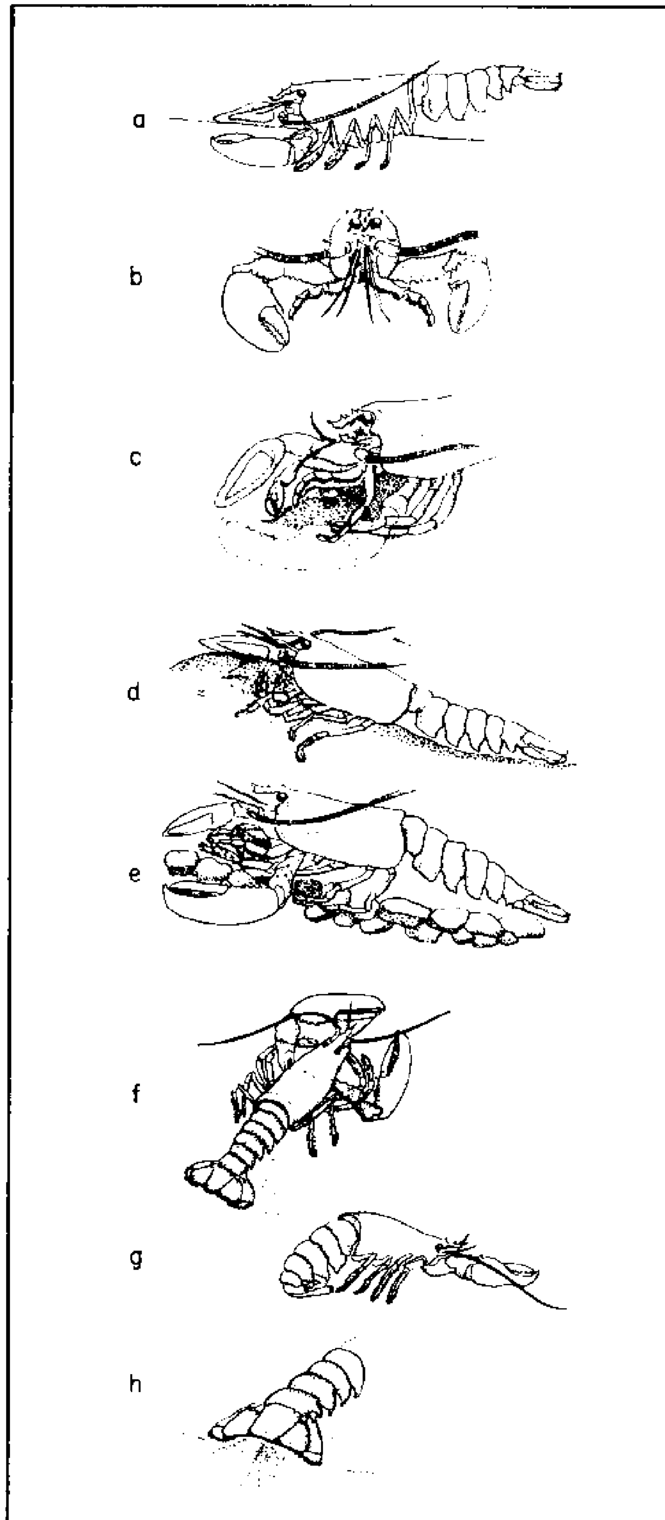


Figure 14. Burrowing behavior of the lobster. A-D) "bulldozing." E) "rock moving." F-G) "backwards dig." H) "pleopod fanning." From Cobb (23).

nel, and probably must have stones or shells on its surface under which the lobster can begin the tunnel (12).

In field observations, and in laboratory experiments on the relationship between the lobster and the size and shape of the burrow it selects, lobsters are generally observed to occupy shelters in which the height is less than the width. The larger the lobster, the larger the shelter. It appears that low, flat shelters are darker — and thus more attractive — than high, square ones (23). If shelter in the form of an artificial reef is provided where none previously existed, lobsters will quickly occupy it (14, 164, 131, 141). This may prove to be a way of increasing lobster populations: increasing the carrying capacity of the environment. Permanent residence, however, probably requires a good food source as well as shelter.
shelter.

Shelters are excavated by means of the following behavioral patterns: "bulldozing" or plowing, with the third maxillipeds and the first one or two pairs of walking legs; "backward digging," or scooping material back through the last pair of legs using the first two or three pairs of legs, followed by "pleopod fanning," straightening the tail and rapid fanning of the swimmerets to cause material to billow out behind the lobster; and "tail carry," or scooping up material with the tail fan and carrying it up to the burrow entrance while bulldozing (Figure 14).

These activities are used in differing proportions, depending on whether gravel, sand, or mud is being excavated. In winter, lobsters will often close the mouth of the burrow with a partition of sediment and debris and remain in the burrow for weeks at a time, apparently almost dormant, especially when the temperature is below 5 °C.

To a certain degree, lobsters are territorial. Only under rare circumstances are two lobsters found in the same burrow, which indicates that burrows are defended no matter how close together they may be. The territory size may be smaller in winter than in summer (164).

Agonistic Behavior. Sixteen agonistic behavior patterns — and their frequencies — have been described (138). Some of them are discussed here.

The most important threat posture is "meral spread," in which the lobster stands with its body raised and claws spread wide, the long axis pointing at the opponent. "Pushing" occurs when the animals push against one another's chelae, usually with the claws closed. When the claws are opened, they occasionally grasp the opponent's claw. Pushing appears to be a test of strength. Lashing at the opponent with the long second antennae — "antenna whipping" — is sometimes seen during pushing.

"Scissoring" occurs when one animal, from the meral spread posture, brings both claws rapidly together either striking or passing just in front of its opponent. An agonistic encounter may be started by an investigatory act, "antenna pointing," in which the lobster directs its second antennae toward the opponent and then makes an "approach" toward it. If the opponent shows avoidance behavior, the animal is said to "follow." Avoidance postures all involve moving away from the opponent, by walking foward, backward, sideways, or by running away. Another defensive maneuver is "abdomen flex," in which the animal jumps off the bottom and brings the antennae, chelae, and walking legs together making a streamlined form. It then rapidly flexes its abdomen and shoots backward through the water.

When confrontations occur, large lobsters tend to defeat smaller ones when there is a weight difference between the two of at least five percent. Males defeat females, and animals with larger claws dominate those of equal carapace length but smaller claws.

There is also an innate factor at work: Some lobsters are more aggressive than others, and these animals can defeat lobsters larger than themselves. Lobsters that have been accustomed to winning their encounters tend to defeat those that are accustomed to losing, even though the "loser" is the larger animal (138). Dominance status is generally established within the first half hour of an encounter and remains stable until the dominant lobster molts, at which point it becomes subordinate (25).

Mating Behavior. A female lobster is only receptive to the male for a period of about 48 hours, just after molting. After the male is attracted to the female by her sex pheromone, the pair stroke each other with their antennae for some time. Then the male rolls the female onto her back, using his walking legs as she assists. The male mounts in a head-to-head position, and copulation occurs with the insertion of the male's intromittent organ into the seminal receptacle.

A large male cannot mate with a female considerably smaller than himself, but a small male can mate with a much larger female (70). When competition between two males for a female occurs, the larger male usually wins. Males are limited in their reproductive capacity: after mating with two females one day, a male was unable to mate the next (70).

Recent observations have been made in large-community tanks that show that the females seek out, court, and take up residence with a male before molting. Copulation takes place after the molting (73).

Fishery

The fishery for *Homarus americanus* is one of the most economically important of the east coast of the North American continent. The continuously increasing demand for lobster is reflected in its increasing value, but not in the number of pounds landed in the United States during the 20-year period 1954-1974 (Figure 15).

Traps. Lobster traps vary in size and design according to local custom. A typical, square Rhode Island lobster pot is shown in Figure 16. Traps typically have one or two openings made of twine that funnel into a section of the trap. Another funnel leads the lobsters into the "parlor," where they remain until the trap is hauled. Generally, the traps are made of oak lath and ballasted with stone or brick to hold them on the bottom. The laths are set far enough apart so that smaller lobsters can escape. Bait, usually fresh trash fish, is hung from the center of the trap. A door at the top allows access so that the fisherman can easily remove the catch and rebait the trap. The two most widely used traps in Maine are either half-round or square in cross-section with one or two parlors. Another design, the "igloo," has not become popular.

Traps used in the offshore fishery are similar in design to the more widely used inshore pots but are larger and sometimes manufactured from plastic coated steel rod and mesh.

Lobsters are brought to wholesalers, who may ship them immediately to other wholesalers or retail outlets, or who may hold them in pounds. These pounds, artificial tidal ponds, allow lobsters caught during peak fishing periods to be stored for later sale at times of higher prices, or, in Canada, during the closed fishing season (93). The possibility of catching lobsters and feeding and holding them through the next molt has often been mentioned, but has been shown to be not economically feasible. Even if fed, there is an overall decrease in total biomass in a group of lobsters held in pounds because of mortality and mutilation (99).

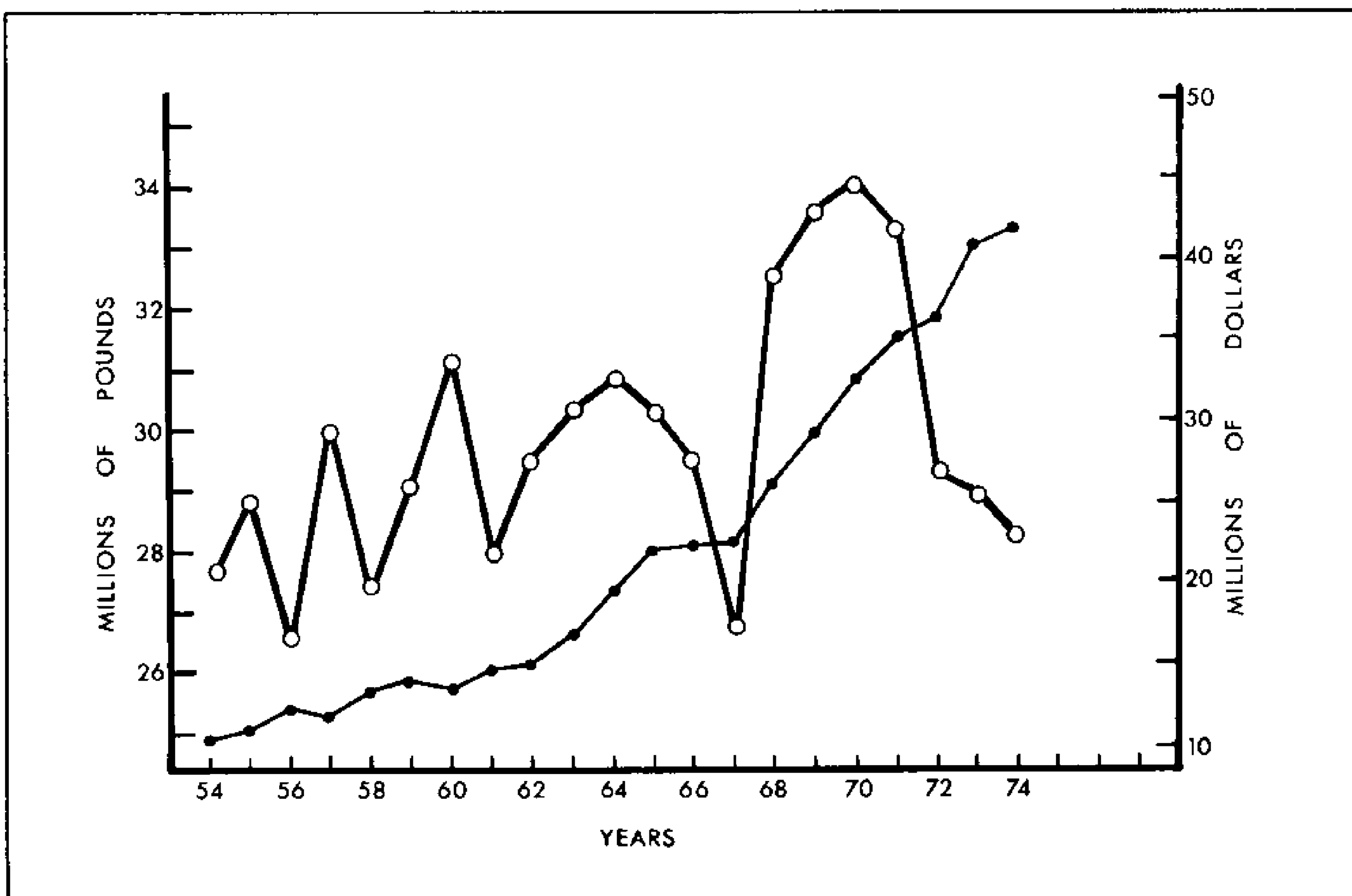


Figure 15. Changes in the catch (open circles, left axis) and value (closed circles, right axis) of the commercial landings of lobsters in the United States.

Offshore Lobsters. Although the majority of lobsters are landed by inshore fishermen working in 5 to 30 meters (15 to 90 feet) of water, there has been a dramatic increase in the number of lobsters landed from offshore fishing grounds since the late 1950's. The grounds extend from Georges Bank — east of Cape Cod — to Chesapeake Bay, at depths of from 150 to 750 meters. They are concentrated in the areas of the submarine canyons (Figure 17). From 1950 to 1967, many vessels used nets (otter trawls), but recently most have switched to large pots set in long strings.

Since 1967, the relative importance of each state's contribution to the inshore fishery has remained fairly constant. But the offshore fishery has grown, and it provides approximately one-third of the total U.S. lobster catch. Most offshore lobsters are probably landed in Rhode Island and Massachusetts. A graph of the estimated offshore landings from 1950 to 1970 appears in Figure 18.

There is little doubt that some separation between offshore and inshore stocks exists. Offshore lobsters are larger, a result of the stocks being exploited only relatively recently. Several morphometric characters indicate shape differences between the lobsters from inshore populations and those from offshore populations. Electrophoretic analyses of lobster blood show other possible differences between inshore and offshore lobsters (10). Several egg-bearing females were captured offshore in Veatch Canyon, tagged, and released in Narragansett Bay; they returned to the canyon. Many others captured were apparently moving toward it (124). When offshore lobsters were captured and released on the offshore fishing grounds, a portion of the tagged animals migrated toward the inshore areas south of Cape Cod in late spring and returned to deeper waters in late fall. It was hypothesized that this migratory behavior is motivated by the search for optimum temperatures, since all were recaptured from waters with a temperature range of 10° to 17° C. This is a much smaller temperature range than that experienced by lobsters remaining inshore, where annual water temperatures vary by approximately 20° C. Offshore lobsters grow faster and molt more frequently than do inshore lobsters (29). Parasites found on and in lobsters differ between inshore and offshore lobster populations (171, 172, 35).

The offshore fishery has been followed by scientists virtually from the start, and it provides an excellent example of the effects of exploitation on a population (137, 109). Veatch and Hudson canyons, closest to shore and presumably most intensively fished, now have smaller-sized lobsters than Lydonia and Corsair canyons. The population in Veatch Canyon showed a marked shift to smaller-sized lobsters from 1956 to 1967 (146). This finding is

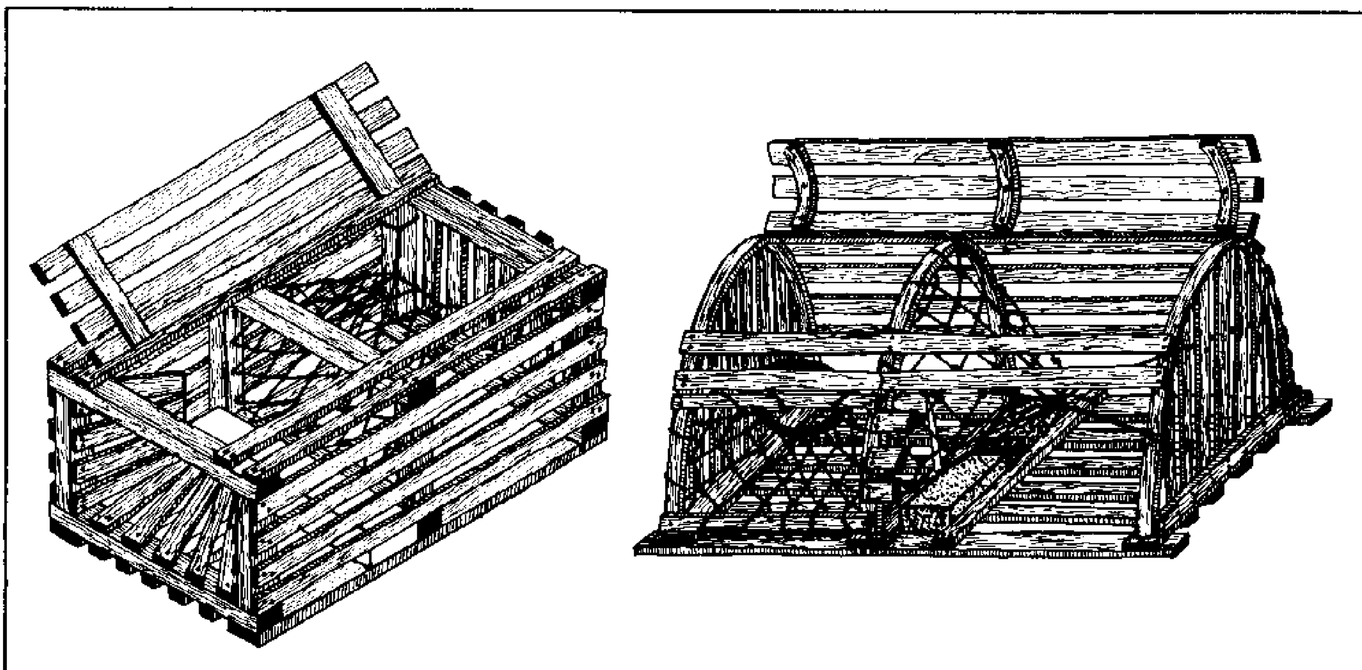


Figure 16. Lobster pots. *Left:* Square design. *Right:* Half-round. The bottom three laths of the half-round have been cutaway for clarity.

consistent with the increase in the proportion of young individuals and decrease in longevity expected of an exploited population. The average daily catch (catch per unit effort) was lowest in canyons most heavily exploited and highest in the canyons farthest from shore, another expected consequence of exploitation.

Tags. Studies in the U.S. and Canada to determine population size, fishing pressure, migration, and size at maturity have involved both the examination of fishermen's catch and the tagging and release of large numbers of lobsters. Many different types of tags have been developed. One of the simplest is an elastic band attached to a numbered, Monel Metal clip. The elastic band is slipped over the rostrum and stretched so that the metal clip hooks over the posterior end of the carapace. This tag is only temporary, as it is lost at molting (177).

The "sphyrion" tag is a numbered, plastic "spaghetti" tag attached to a small stainless steel anchor that is inserted in the dorsal musculature between the carapace and abdomen. This tag is carried through several molts (134). A sonic tag, detectable by acoustic telemetry, has recently been developed. Although expensive, it allows continuous monitoring of the position of the lobster so that its movements can be followed on a daily basis (89).

Recent developments in biochemical analysis for genetic differences have allowed scientists to identify rare genotypes. It is possible that these rare types could be selectively bred and released, using the rare genotypes as a biological tag (65a). The simplest suggestion of this type has been to breed color variants such as red or mottled lobsters.

Migrations. Tagging studies on inshore lobsters, done primarily by Canadian investigators, show that the animals do not move more than 10 to 15 miles from the release site. In other words, populations tend to be local (180, 178, 28). There are some indications, however, that large inshore lobsters may move remarkably long distances: Several, tagged and released in northern Maine, were recaptured in Massachusetts, their having travelled between 75 and 138 nautical miles (38). Rhode Island lobsters appear to move into Narragansett Bay in the spring and out again in the fall, but distance traveled is unknown (75).

Fishing Pressure. The fishing pressure on lobsters is intense; between 70 and 90 percent of all the legal-sized

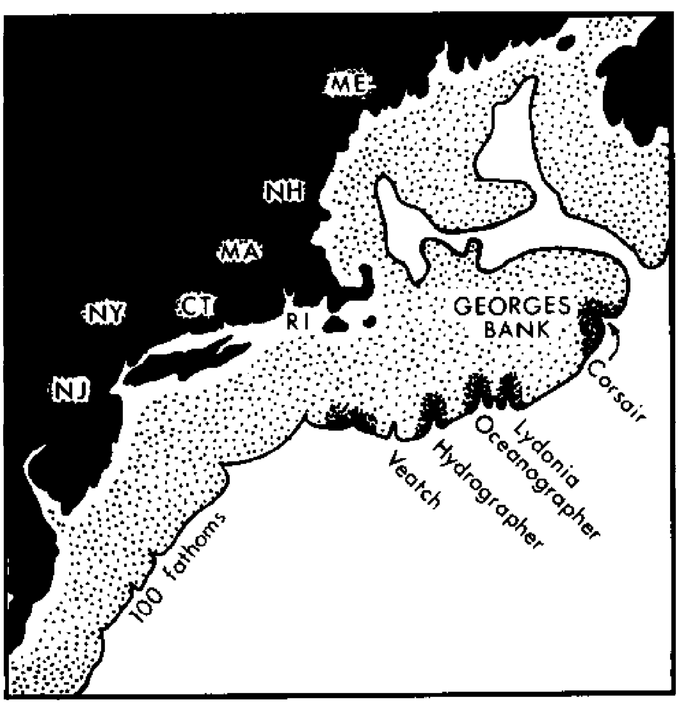


Figure 17. The location of submarine canyons at the edge of the continental shelf, where most offshore lobsters are caught.

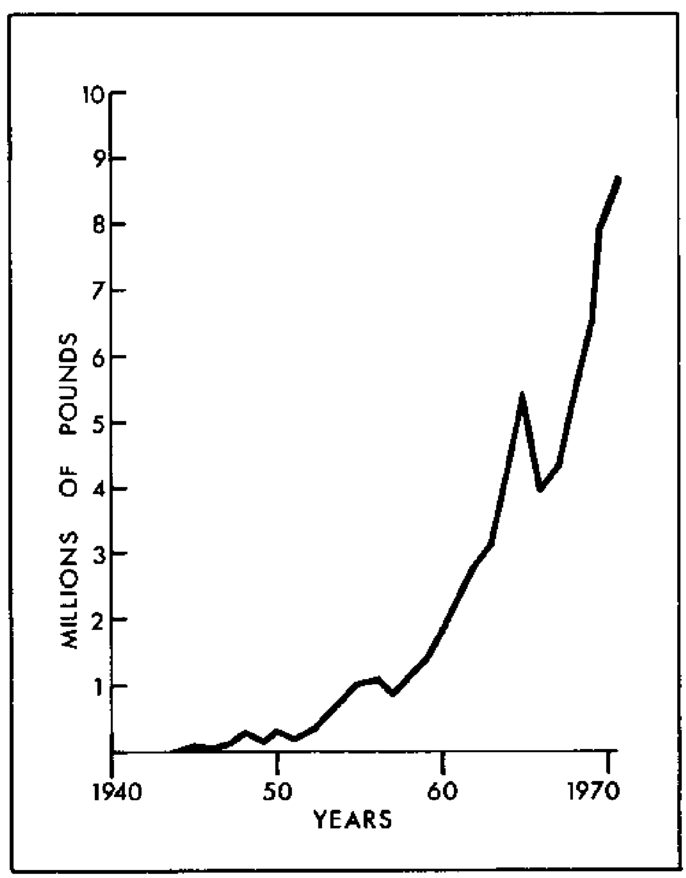


Figure 18. Estimated increase in catch of offshore lobsters, 1940-1970.

inshore lobsters are taken each year. Calculations by the National Marine Fisheries Service show that the fishable stock of U.S. inshore lobsters is consistent with the maximum sustainable yield (MSY). That is, the greatest amount that can be taken each year on a continuing basis is 31 million pounds (55). The fishery has probably been oversaturated since the end of World War II (53), and there are at least enough traps and boats in use now to catch lobsters at the MSY level. In fact, recent annual catch per trap has declined from 50.2 pounds in 1951 to a low of 25.4 pounds in 1969 (55).

What factors have led to the complete capitalization of the industry, the full exploitation of the resource, and the concurrent decline in catch per unit effort?

First, in the United States, no one who can pay the relatively low price of a license and can afford to buy traps is denied access to the fishery. Nor, with a minor exception, is there any closed season.

Second, there is a marked increase in consumer demand for all species of lobster, not just *Homarus americanus*.

And third, there has been a drop in seawater temperature — a factor that some scientists believe contributes to the decline in the catch. Robert Dow, of the Maine Department of Marine Resources, attributes the decline over the past 20 years, despite the increase in fishing effort, to a gradual cooling of ocean waters (37).

A model of the lobster-fishing industry has been developed that shows that, since World War II, the catch size has not depended upon the amount of effort. It can best be predicted by the mean, bottom-water temperatures of the months from January to June of the six, seven or eight prior years, and the mean temperature (January-June) of the present year (53). It was pointed out that the water temperature affects a lobster's rate of walking, and so its "catchability" (108, 115).

Regulations. Certain regulations have been issued to protect the stock of lobsters. All states impose a minimum legal catch size, varying from 3-1/16 inches to 3-3/16 inches in carapace length (CL). The intention of this regulation is to allow at least some of the females to breed before being caught. The size of the female at the time at which eggs are first extruded, although variable with water temperature, is generally above this minimum size, usually about 3-1/2 inches CL.

Krouse (82) has argued for a larger minimum size in Maine. Maine also has a "double gauge" law, protecting lobsters above five inches in carapace length from capture on the assumption that larger lobsters carry more eggs and thus make a greater contribution to the fecundity of the stock. The value of this law has been debated by those who point out that the number of females above five inches CL makes up a tiny proportion of the fishery (123). All states have regulations protecting egg-carrying females, and there are severe penalties for possessing an "egger" or for brushing off eggs. A modeling study (123) has demonstrated the value of this regulation in increasing the fecundity of the stock, although some researchers do not agree about its applicability to Canadian lobster populations (179).

Economics. Economic aspects of the fishery have been examined in detail by Canadian and American economists (11, 34, 69, 167) and will not be treated here. A bioeconomic model has been developed to review several possible management strategies, including methods of imposing license fees on traps, issuing "stock certificates" that would allow each fisherman a share of the existing resource, the auctioning of fishing licenses to achieve a limited-entry fishery, and no management at all (122). No recommendations were made, but it was pointed out that, without some sort of management, the lobster fishery will become increasingly over-capitalized as demand and fishing pressure increase.

Aquaculture

The apparent decline in stocks, coupled with increasing consumer demand, has generated a great deal of interest in lobster aquaculture in the last few years. As a result, a considerable amount of federal money has recently been made available for research into the various biological, technological, and economic aspects of lobster aquaculture in the Unites States and Canada.

As early as 1885, the U.S. Fisheries Commission began a program of hatching eggs from berried females and releasing the first stage larvae into the natural environment. By the early 1900's there were many hatcheries in New England and Canada, but by about 1917 most were discontinued because they could not be justified either biologically or economically (9). A notable exception was the lobster hatchery on Martha's Vineyard, maintained by the Commonwealth of Massachusetts. It is from this establishment — and because of the efforts of its director, John Hughes — that much of the knowledge of and encouragement for lobster aquaculture originally came. Hughes and his colleagues spent years learning how to encourage lobsters to mate, lay and hatch eggs, and to rear larvae and juveniles. The development of lobster aquaculture programs was greatly enhanced by the realization that the time required to grow a lobster to one-pound size may be reduced from five to about two years by rearing them in artificially warmed water (72).

Criteria for Aquaculture Potential

Certain criteria must be met before a marine animal can be considered a likely candidate for aquaculture. These criteria follow (57, 92):

1. Spawning and gametogenesis controllable under laboratory conditions
2. Simple larval development
3. Fast growth rate
4. High food conversion efficiency
5. Satisfactory feeds known and commercially available at competitive prices
6. An animal indigenous to the region
7. High retail prices
8. A hardy organism resistant to stress induced by confinement
9. The ability to hold at high density
10. Resistance to disease

The lobster does not score high in any of these categories, except for the retail price category. Nevertheless, the decline in lobster stocks coupled with an increase in consumer demand has persuaded many that the lobster is an adequate candidate for culturing. The life cycle of the lobster is well known, and it can easily be completed under controlled laboratory conditions and shortened by about 50 percent by optimizing temperature and feeding. It appears that, once the biological problems of controlled spawning, nutrition, and disease are solved, the raising of lobsters will become mostly a technological problem.

What are the specific problems that must be solved before lobster culture can become a reality?

Nutrition. Providing adequate nutrition at low cost is a primary consideration. So far, the foods that give the highest growth rates are lobster flesh, the West Coast pelagic red crab *(Pleuroncodes planipes)*, and live or frozen adult brine shrimp *(Artemia salina)*. Lobster flesh is clearly unacceptable as food; the availability of *Pleuroncodes* is widely variable, and *Artemia* purchased commercially costs about $1 a pound. The conversion ratio of wet-weight-of-food to wet-weight-of-lobster is estimated at approximately 4:1 (88). Obviously, having to spend four dollars to feed a one-pound lobster makes the use of brine shrimp as a food source economically unsatisfactory.

Currently, two approaches are being made in the direction of a possible solution. The first approach involves testing the influence on growth rates of several natural and man-made foods. The second is to design artificial diets that can be tested for growth rate and compared to the standard of a brine shrimp diet.

Adult lobsters require levels of dietary protein as high as 60 percent and have additional requirements for lipids and cholesterol (16, 17). It appears that brine shrimp provide a biologically adequate diet for all stages of the lobster's life cycle, from larva to adult. The frequency and amount of feeding may vary, but feeding five percent of the body weight once a day appears to be adequate, except in the larval stages where more frequent feeding is required to reduce cannibalism.

Disease. The greatest obstacle to commercial aquaculture may be disease. When lobsters are held under high-density, stressful conditions, diseases that are unknown in natural environments often show up.

Gaffkemia, possibly the best known, is a usually lethal bacterial infection of the hemolymph (147, 161). It is transmitted only through recent ruptures in the integument, such as the wounds caused by the use of wooden pegs to immobilize the chelae when lobsters are kept in holding pens (158).

The incidence of this disease in natural settings is generally low, but may go as high as 39 percent of the population (162). Cooler temperatures tend to slow the progress of the disease but not stop it (160). Starved lobsters infected with gaffkemia survive longer than fed ones because, when fed, the blood has a richer nutrient supply and can support a more rapid development of the pathogen (163). Lowering the salinity of the water after infection also increases the time course of the disease (154).

An immunization technique for gaffkemia has been developed (77, 136) and an antibiotic, vancomycin, is effective in treating the early stages of the disease (155). Additionally, lobsters to be introduced into a culture system can be screened for the presence of the pathogen. Thus, it appears that gaffkemia should not be a major problem in aquaculture of lobsters.

In the larval stages, an infestation by the common filamentous bacterium *Leucothrix mucor* can cause high mortality due to anoxia when lobster gill membranes become fouled (76). *Leucothrix* and other filamentous microorganisms apparently derive their nutrients from the surrounding water, and their growth is enhanced when the concentration of dissolved organic matter in the water rises (50). Penicillin and streptomycin have been recommended for treatment of infection (76), but this treatment allows other microorganisms to invade, often with equally destructive results.

One fungus, *Lagendinium* sp., invades and completely destroys the tissues of larval lobsters. Another fungus, *Haliphthoros milfordensis*, breaks down chitin and is responsible for occasional mortalities in juvenile lobsters. A shell disease of wild lobsters caused by chitinivorous bacteria sometimes reaches epidemic proportions in lobster pounds (66).

Cultured lobsters occasionally succumb to "gas disease." This is not, in fact, a disease, but a condition caused by minute gas bubbles small enough to pass from the water through the gill membranes to the hemolymph. The bubbles collect and form larger bubbles, emboli, in the circulatory system. In the early stages, this condition can be recognized by the small, whitish bubbles that form in the lobster's eye. In more advanced cases, death results, usually accompanied by lifting of the carapace. The bubbles in the water are a result of the supersaturation of gases, due either to heating the water or to a small leak on the suction side of the pumping system.

As with all disease, prevention is by far the best procedure. This is especially true for lobster culture; For most diseases, no cure is known. Water quality and general cleanliness must be stressed as the key to disease-free systems. Seawater can be irradiated with ultraviolet light to kill bacteria, and mechanical and biological filtration must be used to maintain a high level of water purity (51).

Controlled Spawning. Brood stocks must be managed so that young are available year-round for continuous production. Lobsters have been mated in captivity, and the females have laid and hatched eggs. It is possible to complete the entire life cycle in the laboratory. It is also possible to speed up egg development by holding wild, winter caught lobsters in warm water.

But the process of maturation and egg development is a complex one (4). The first time a female extrudes eggs is in the fall, about a year after the puberty molt (the time at which ovarian vitellogenesis started). The female molts after the eggs are hatched early the following summer. The ovary then starts its second cycle, with the result that both the molt cycle and the ovarian cycle approach completion the following summer. This is not critical, except that if the ovaries develop too fast — so that egg laying occurs before molting — the gravid ovary will be reabsorbed and no eggs will be produced that year. This complication may result when females are "pushed" in warm water to achieve earlier egg extrusion. A female Specific Protein (FSP) has been identified in the blood before spawning. Measuring the concentration of FSP may allow prediction of spawning time (4).

At this time, the control of spawning and production of eggs and larvae on a year-round basis is not possible. It is only through further research into the reproductive physiology of the lobster that the ability to manage brood stock will be realized.

Genetics. Genetic alteration of growth rate, disease resistance, nutritional requirements, and behavior may all be required. This may be accomplished through both basic research and simple selective breeding techniques.

Relatively little is known about the genetics of the lobster. Studies of natural populations have shown morphometric differences between geographically separated stocks. There have been consistent reports of lobsters with odd coloration. It is not known whether these differences are due to environmental or genetic factors.

A program of genetic research has been initiated at the University of California (Davis). A survey of geographically separate lobster populations has been conducted using gel electrophoretic techniques to detect genetic differences in enzymes and proteins. In general, the results show that lobster populations have only a moderate amount of genetic variability when compared with other invertebrates.

The researchers found one gene whose allele frequencies differ among populations from Massachusetts, Prince Edward Island, and the offshore canyon populations (169). They have also developed a possible technique for detecting progeny of a specific female by examining frequency of "allozymes" — allelic enzyme variants — and using them as a natural tag. These allozymes occur with predictable frequency in the lobster population; if an individual differs from what is expected of the population, it, in effect, carries a natural and permanent tag. This information may be used to monitor the survival and dispersion of lobsters, as well as the efficiency of restocking procedures (65a). There is some difference between the American and European lobster. Hybridizing the two species may lead to increased heterozygosity; this is often correlated with increased yield in plant and animal breeding studies.

Water Quality. Although high levels of water quality must be maintained (because of toxic metabolic wastes and because water discharged from any commercial operation must meet standards set by the Environmental Protection Agency) lobsters can survive in water with quite high levels of nitrogenous compounds. In fact they can tolerate concentrations of ammonia, nitrate, and nitrite considerably higher than that usually expected under culture conditions. For 24 hours, most juvenile lobsters of one to three grams will survive concentrations of ammonia (NH_4) below 250 mg./1. if other conditions are optimal. However, longer exposure (96 hrs.) to ammonia at lower concentrations (1.2 to 1.4 mg./1.) causes death (61).

Not enough is yet known about the long-term growth and survival of lobsters in water of low quality to allow for any definitive statements about it. But there is no doubt that disease occurs with much more regularity when water quality is poor, particularly when the dissolved organic content is high. It is therefore important for a culture system to maintain the highest water-quality standards possible until further research can be done.

Holding Systems. If lobsters are held in groups, behavioral problems ensue. If held individually, a complex system of containerization, food delivery, and water circulation must be designed.

The culture systems thus far envisioned take three approaches: individual containers, communal tanks, and polyculture. Most of the investigators working with lobster culture at this time lean toward communal rearing of the larval stages, followed by separation of the juveniles into individual containers.

Lobster larvae, and many other aquatic invertebrates, are reared in so-called "Hughes Tanks" — cylindrical, fiberglass tubs designed by John Hughes (71). These tanks circulate the water to keep the larvae in constant motion, a requirement necessary to increase food availability and to decrease mortality due to cannibalism. A recirculating system (126a) incorporating these tanks is shown in Figure 19. An automatic feeder (Figure 19) that can deliver brine shrimp at specified intervals can also be added to this system (139). When lobsters are grown in a culture system of this type — with excellent water quality and liberal amounts of live, adult brine shrimp for food — a survival rate of 90 percent to the fourth stage may be attained.

Most current techniques for raising juveniles involve single containers in which the lobsters are held individually. The major problems are that this method uses a great deal of space, and that food delivery and the main-

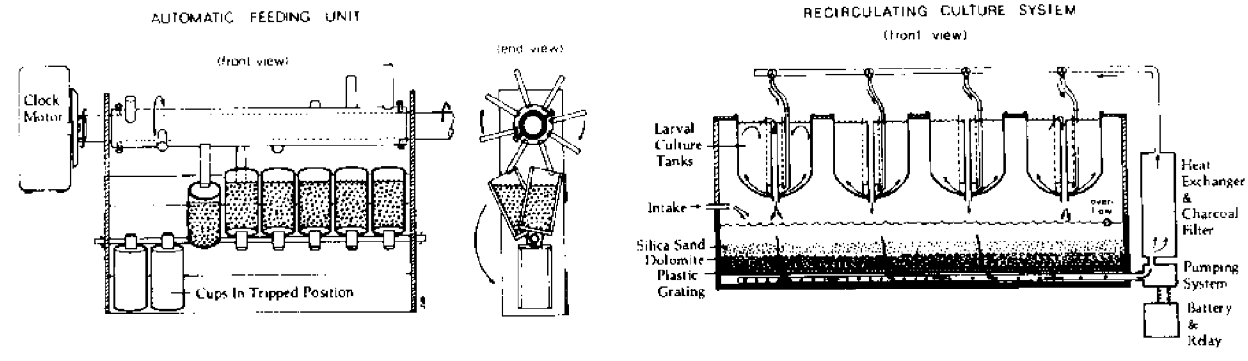


Figure 19. *Left*: Automatic food dispensing unit. *Right*: Larval culture system similar to that in use at the University of Rhode Island.

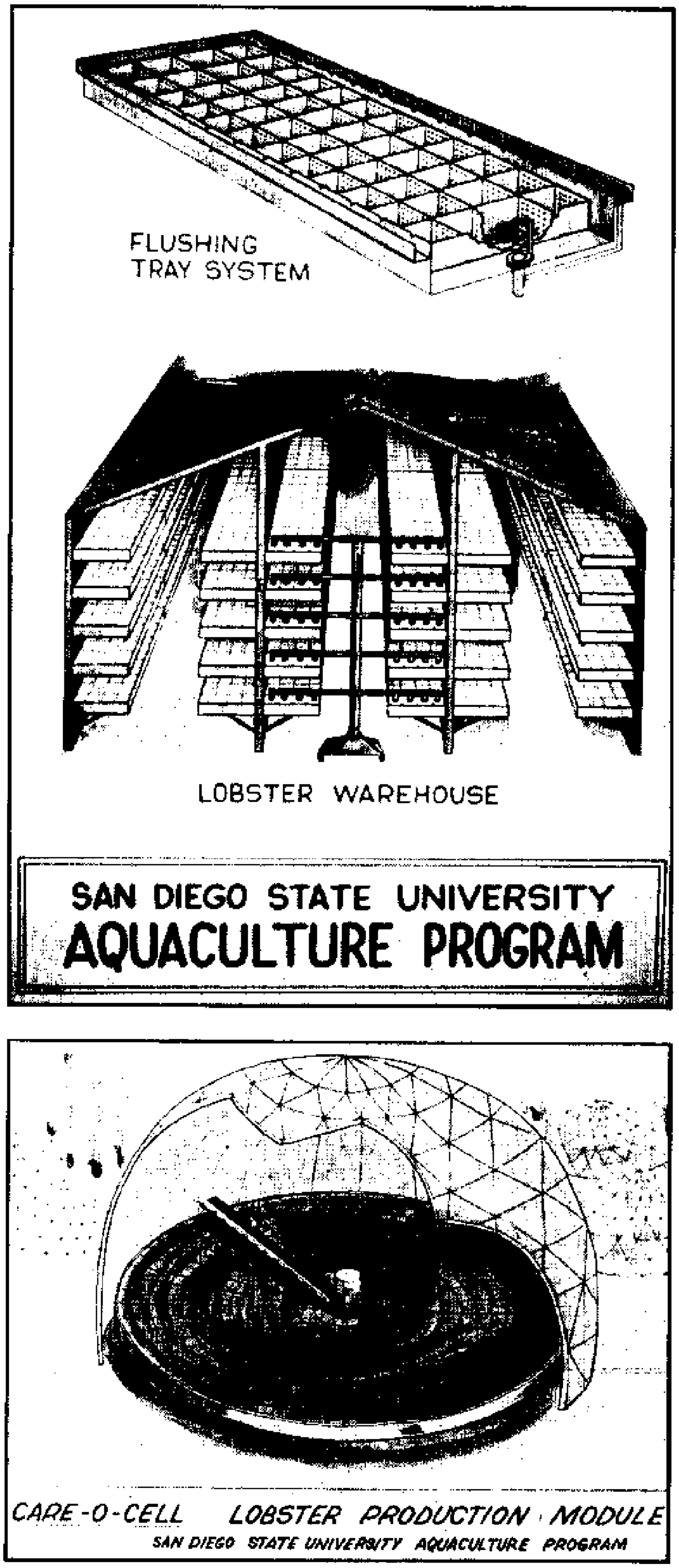


Figure 20. "Raceway" and "Care-o-cell" designs for lobster aquaculture facilities as envisioned by aquaculturists at San Diego State University.

tenance of clean conditions are more difficult than in communal systems. Several designs are now being tried; basically, they have two configurations.

The "raceway" design (Figure 20) sets one or several containers across a long trough or water table. Water flows in one end and out the other. The containers may have screened sides or bottoms. Flushing is accomplished by rapidly lowering the water level at specified time intervals. Construction material is generally a low-cost plastic (173). One inexpensive system for holding small juveniles uses plastic net tubing divided to form modular habitats (18).

The "care-o'cell" design (Figure 20) is essentially a shallow, round tank based upon the design of a primary, sewage-treatment clarifier. In it floats a revolving group of screened-bottom rearing containers (173). Angled-water jets, from a radius arm above the containers, supply water and keep the arm in motion. Feeding has been done by hand, but an automated system is not difficult to envision. Variations of these approaches have sought to create more efficient use of facility space and to permit simultaneous feeding of many animals through highly engineered stacking systems (Figure 21). These variations are mostly proprietary designs created in the private sector and have patents issued or pending.

Space limitation is apparently a serious factor. All the investigators working on lobster culture have shown that growth slows long before the container size becomes physically limiting. The shape of the container has no effect on growth rate (145).

Some investigators have attempted mass-rearing techniques for juveniles in communal tanks. Mortality is relatively high in such systems, whether or not shelter is provided. Lobsters held in communal conditions had mortality rates as high as 30 percent (128), with most of the mortality due to cannibalism at the time of molting. The degree of molt synchrony in the group was positively correlated with survival. Lobsters held over long periods of time showed higher survival when at least two shelters were provided per animal and when the space provided per lobster was greatest (173).

Lower levels of locomotor activity have been observed in communally held juveniles than in individually held lobsters, and the presence of shelter tended to synchronize activity with the light cycle. The amount of aggression in communally held lobsters is highest when they are first put together and decreases with time to a relatively low level under moderate stocking densities. This is probably due to the formation of dominance-subordinate relationships (181).

When two lobsters are held together, one becomes dominant and molts sooner than the subordinate lobster (20, 22, 24, 25). This effect is also seen in larger groups when one or two animals tend to grow faster than all the others. When lobsters are held communally, aggressiveness decreases but does not cease (40). Decreasing temperature from 10° to 5°C will also reduce aggressiveness, as will housing lobsters individually but within sight of each other (68).

Because of behavioral problems, mass-rearing systems for the entire growth period of lobsters do not seem feasible at this time. There is no doubt that at sufficiently low densities lobsters can be cultured communally, but the space requirements would be excessive. There are many advantages to mass-rearing systems, however, and attempts should continue toward an understanding of lobster behavior, particularly with regard to aggression within large groups.

A polyculture approach is being attempted by the Environmental Systems Laboratory of the Woods Hole Oceanographic Institution. There, oysters are grown in cement raceways provided with heated water during the winter months. Additional populations of amphipods, blue mussels, and polychaete worms develop in the raceways and serve as a food source. High growth rates have been reported (112), but at densities that are too low for intensive lobster culture. As an addition to such a polyculture system, however, the lobster may be ideal.

Economics. Not only must an aquacultural operation be able to rear the animals, it must also be able to produce a product that is cost competitive with wild-caught stock. This requires continual cost evaluation through the research period, although cost effectiveness may not always be compatible with biological optimization.

At this time, not enough is known about the biology and technology of lobster culture to make predictions concerning the economics of lobster rearing. A mathematical model of a lobster aquaculture facility has been constructed (13), based on optimal control theory that can identify the areas of research most important to the development of the aquaculture system. The model can also be used to predict the proper temperature, feed ration, and space that should be provided the lobsters on a cost basis rather than on a biological basis. The point of such a model is that the production of an economically competitive lobster, not necessarily the fastest growing one, is the important factor.

For example, lobsters fed on brine shrimp at $1.00 a pound may reach market size in two years, whereas those fed another food at 15 cents a pound may take 2½ years. The optimization model, taking into account the increased time and associated increased cost of labor and heat, can predict which food it would be better to feed.

Predictions have been made that lobster farming is a distinct possibility, and that sooner or later lobsters will be raised the way chickens are now. Many of the problems facing lobster culturists today are similar to those that fish culturists, chicken farmers, and other animal husbandmen have had to overcome. With the price of lobster being driven up by increasing demand and decreasing landings, the cost of cultured lobsters may become favorably comparable to the price of native lobsters. It has been predicted that there may be as much as a 20-40 million pound difference between the native fishery supply and consumer demand by the mid 1980's (15a, 112a). If commercial aquaculture of lobsters does become a reality, it will only partially make up the difference in the foreseeable future. As a benefit to the fishery, the excess of post-larval lobsters produced by an aquaculture facility could be released to the natural environment under the supervision of federal or state officials.

Currently, pilot-scale lobster farms are being planned in California and Connecticut, and one has been in operation in Maine (under special license of the Maine Department of Marine Resources) since mid-1975. From these, much more will become known about the biological, technological, and economic problems of lobster aquaculture.

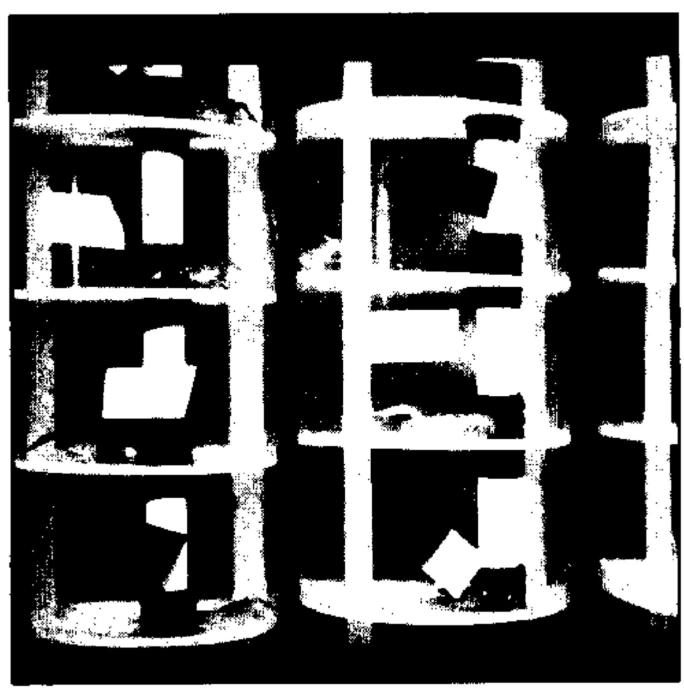


Figure 21. Patented lobster culture system.

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