

Homarid Lobster Hatcheries: Their History and Role in Research, Management, and Aquaculture

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Introduction

Most historical reviews on lobster, *Homarus* spp., hatcheries have dealt with the specific objectives of hatchery operation: hatching eggs and release of Stage I larvae or the rearing and release of Stage IV postlarvae (Nigrelli, 1936; Carlson, 1954; Thomas, 1964; Wilder, 1972; Dexter, 1986). Kenslor (1970) reviewed lobster hatcheries and, to a limited extent, the benefits accruing

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from the scientific research they conducted. Bardach et al. (1972) emphasized the activities conducted at the hatchery on Martha's Vineyard, Mass. In each case, the reviews focused on the economic and biological successes or failures of hatchery efforts (see Mead, 1910; Scattergood, 1949b; Taylor, 1950; Carlson, 1955; Taylor and Dow, 1958; Prudden, 1962; Dow, 1969). However, the current usefulness of lobster hatcheries in advancing knowledge about the life-history of homarid lobsters has not been fully explored.

From as early as 1858, experimental lobster culture has provided a large volume of information on the species' life history (Scattergood, 1949a; Lewis, 1970; Nowak, 1972). Anatomy, physiology, development, general habits, behavior, and preferred habitats were

investigated within these hatchery settings; questions concerning the state of the fishery and its preservation were also addressed (Herrick, 1894, 1895, 1911a; Scattergood, 1949b). The information gained thus far (reviewed in Cobb, 1976; Cobb and Phillips, 1980; McVey, 1983; Cobb and Wang, 1985; D'Abramo and Conklin, 1985; Mackenzie and Moring, 1985; Waddy, 1988; Aiken and Waddy, 1989, 1995; Lee and Wickins, 1992; Chang and Conklin, 1993; Conklin and Chang, 1993; Factor, 1995; Waddy and Aiken, 1995) has accumulated from over 100 years of detailed experiments. In retrospect, the facts obtained from the early work of hatcheries formed a sound foundation from which current lobster research and management evolved.

This paper reviews and summarizes the literature on past and present homarid lobster culture, hatchery activities, and stock enhancement programs, and gives recommendations for their future use. Most of the emphasis will be on the American lobster, *Homarus americanus* (Fig. 1) with references made to comparable data for *H. gammarus* (previously *H. vulgaris*). The three species of clawed lobsters, *H. americanus*, *H. gammarus*, and *Nephrops norvegicus*, have similar morphological and developmental trends (Gruffydd et al., 1975; Howard, 1989). Each species has a prelarval stage followed by three larval stages and then a postlarval stage which resembles the adult. These developmental similarities imply behavioral and ecological similarities (Berrill, 1974). Thus, culture techniques and information obtained for one species often can be directly applicable to the others (Van Olst et al., 1980; Cobb and Wang, 1985).

Although this is not an exhaustive review of all hatchery-inspired experi-

ABSTRACT—This paper provides a historical review of homarid lobster fisheries, the development and usage of lobster hatcheries, and much of the research influenced by hatchery-initiated studies on natural history, physiology, and morphological development of the lobster, *Homarus* spp. Few commercial lobster hatcheries exist in the world today, yet their potential usage in restocking efforts in various countries is constantly being reexamined, particularly when natural stocks are considered "overfished." Furthermore, many individual researchers working on homarid lobsters use small-scale hatchery operations to provide the animals necessary for their work as well as animals reared and provided by various governmental agencies interested in specific projects on larvae, postlarvae, or juveniles. Such researchers can benefit from the information in this review and can avoid many pitfalls previously documented.

The development of hatcheries and the experimental studies that were generated from their activities have had a direct impact on much of the research on lobsters. The past work arising from hatchery operations—

descriptions of life stages, behavior, physiology, etc.—has generally been confirmed rather than refuted and has stimulated further research important for an understanding of the life history of homarid lobsters. The connections between homarid fisheries and hatchery operations (i.e. culturing of the lobsters), whether small- or large-scale for field and laboratory research, are important to understand so that better tools for fishery management can be developed. This review tries to provide such connections. However, the rearing techniques in use in today's hatcheries—most of which are relics from the past—are clearly not efficient enough for large-scale commercial aquaculture of lobsters or even for current restocking efforts practiced by several countries today. If hatcheries are to be used to supplement homarid stocks, to restock areas that were overfished, or to reintroduce species into their historical ranges, there is a clear need to further develop culture techniques. This review should help in assessments of culturing techniques for *Homarus* spp. and provide a reference source for researchers or governmental agencies wishing to avoid repeating previous mistakes.

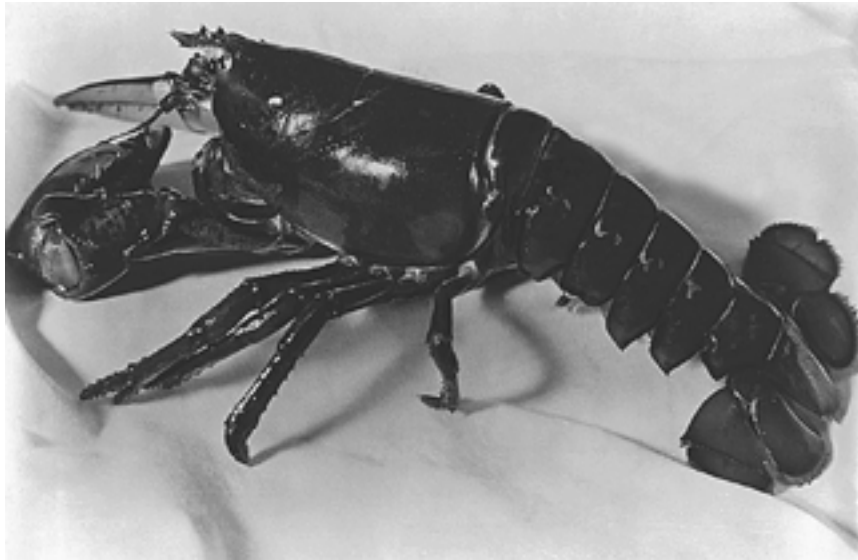


Figure 1.—American lobster, *Homarus americanus*.

ments and their results, this paper will provide the reader with an insight into how valuable the hatcheries have been and what their future role could be. For the enthusiast wishing to pursue the subject further, a bibliography of well over 400 literature citations and selected references is also given. To adequately review the origins of lobster hatcheries, we must start with a brief overview of the history of lobster fisheries.

History of Lobster Fisheries

The American lobster and its European counterpart, *H. gammarus*, are among nature's most valuable resources for commercial and, to a limited extent, recreational fishermen. Until this century, these lobsters have been able to survive the hazards of nature and mankind, despite commercial fishing efforts which began as early as the 17th century (Herrick, 1911a; Dow, 1949; DeWolf, 1974; Bennett, 1980; Dow, 1980). They were reported as easily captured food sources in both Canada and New England in the early 1600's and were so plentiful that they were also used as fish bait and fertilizer in the 1800's (DeWolf, 1974; Martin and Lipfert, 1985).

During the summer months, lobsters were so common in the shallow littoral zone that fishermen often gathered them by hand, dip net, and spear, or they

were gaffed with a hook attached to a pole nearshore (Rathbun, 1884a, 1887; Cobb, 1901; Herrick, 1911a; Dow, 1949; Krouse, 1989; White, 1991). Herrick (1895) attributed this abundance of nearshore lobsters to a bountiful food supply, but explained that the number and persistence of lobstermen had profound effects upon the abundance of larger lobsters.

Lobsters were also taken by hoop nets used from small boats near the shoreline (Cobb, 1901; Herrick, 1911a; Dow, 1949; Krouse, 1989). Hoop nets were labor intensive due to their construction—they consisted of a 70 cm diameter iron hoop over which two half wooden hoops crossed. The iron hoop was attached to a shallow net bag and it was baited at the intersection of the wooden hoops. Because lobsters could exit as easily as they could enter the nets, fishermen had to pull the nets every 10–30 minutes (Rathbun, 1887; Miller, 1995).

Around 1840, fishermen modified those hand practices to achieve more efficiency and began utilizing a trap or "pot" to capture lobsters (Herrick, 1911a; Dow, 1949; Krouse, 1989). Ranging in sizes from 0.76 to 1.2 m (2.49 to 3.94 feet) long, 61 cm (24 inches) wide, 45.7 cm (18 inches) high, these pots were made of wooden laths and

cotton or manila cord heads, tarred and strung to form a "funnel," which was attached to an entrance ring made of spruce 15.2 cm (6 inches) in diameter (Herrick, 1911a). As bait, fishermen used salted or fresh herring, halibut, hake, and cod heads (Cobb, 1901; Herrick, 1911a; Dow, 1980), or, to a lesser degree, synthetic substances, which consisted of a cloth bag filled with sand and saturated with uncooked herring oil, or mackerel pellets saturated with redfish oil (Prudden, 1962; Dow, 1980). Baited pots were weighted and then placed on the sea bottom, either singly, doubly, or by trawl (8–40 pots) with a rope or cord attached to a wooden float (buoy). Hundreds of traps were pulled (hauled to the boat) by hand several times a day, while others were left overnight (Herrick, 1911a; Dow, 1949). When lobsters seemed to be less abundant or more widely scattered in the 1880's, fishermen returned to the less common and older practice of setting pots singly and altering pot position daily in hopes of capturing more lobsters by covering more fishing areas (Rathbun, 1884a) (Fig. 2).

An ever increasing demand for the lobster as a source of food resulted in tremendous increases in fishing intensity and annual landings. The change from hoop nets to pots allowed so many lobsters to be captured that supply sometimes exceeded demand, and, in the United States, lobsters were so abundant that they were used as agricultural fertilizer, cod bait, and for semicommercial purposes in the 18th and 19th centuries (Dow, 1980). By the early 19th century, what seemed to be an inexhaustible supply of lobsters had begun to decline (Wood, 1869; Rathbun, 1884b). In an effort to ensure a continuous supply of lobsters, protective measures were passed in state legislatures which included licensing fishermen, leaving or returning to the sea "berried" females, closing certain fishing areas during particular seasons, limiting the size of lobsters caught, and culturing.

Today, the pot shape basically remains unchanged, being rectangular (most common), half-round, or squared (Firth, 1950; Everett, 1972; Dow, 1980; Krouse, 1989; Miller, 1995); however, instead

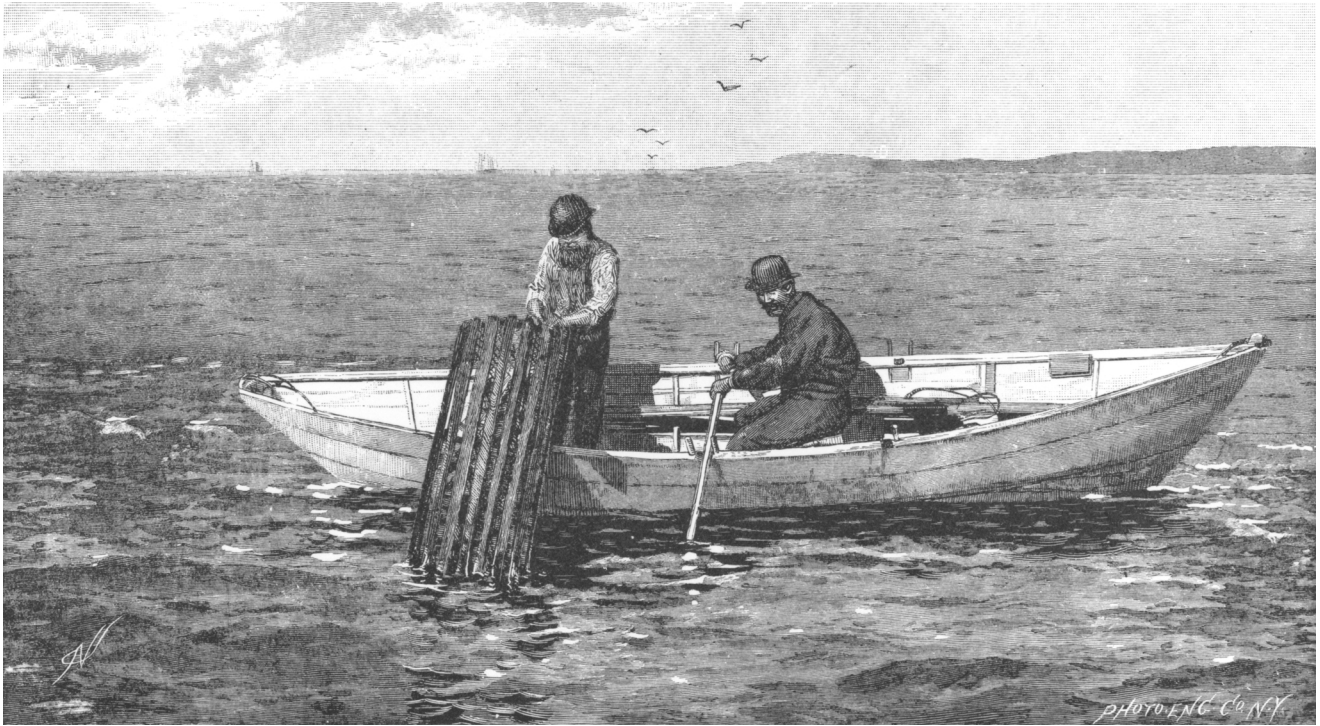


Figure 2.—Above: Dory fishermen hauling lobster pots off Cape Ann, Mass. Below: Lobster fishing boats of Bristol, Maine. (Goode, 1887).

of being made of wood, the frames may now be made of aluminum, plastic, or vinyl-coated wire frames (Krouse, 1989) (Fig. 3). Nylon or plastic replaced the cotton and manila cord heads, and polypropylene is used instead of manila for the warps (Prudden, 1962; Krouse, 1989). Wooden or cork buoys were replaced by styrofoam or plastic buoys (Scarratt, 1980). Perhaps the most significant change was the addition of an inner chamber, or “parlor” (Fig. 3b, c), which increased the efficiency of the pot, as lobsters could not fall out of the end funnel during hauling and were less likely to escape on their own (Knight, 1918; Krouse, 1989; Miller, 1995). To reduce ghost fishing by lost pots and to allow many undersized lobsters to escape before hauling, escape vents were added into the design of the trap in the 1980’s and trap doors or “ghost” panels are now closed with a material that biodegrades in 1 year (Miller, 1995).

In addition, the row boats and sailing dories previously used by fishermen (Fig. 3) have been replaced by faster and larger boats, averaging at least 11 m (36 feet) in length (Gates and D’Eugenio, 1975; Pringle and Burke, 1993), equipped with electronic devices (e.g. radio, cellular phones, depth sounders, LORAN, GPS, radar) and sleeping berths. Small gasoline engines, used as early as 1900, were replaced by diesel engines in the 1970’s (Miller, 1995). Belt-driven haulers were also replaced by electric or hydraulic pot haulers (Krouse, 1989; Miller, 1995). While many pots are still baited with 2–4 fresh or salted fish, some lobstermen are once again using synthetic baits made from animal hide which are now proving successful (Stevens, 1993). These synthetic baits are cut into 8-ounce (227 g) strips, soaked in a salt solution to stabilize and preserve them, and infused with fish oils. One pound of this bait will fish a pot for 1 month (Stevens, 1993). Because of these modern materials and methods, fishermen can now fish further from shore, fish more pots at a faster rate, and spend less time repairing pots.

Early Protective Measures

The earliest lobster protective measure, enacted by Massachusetts in 1812,

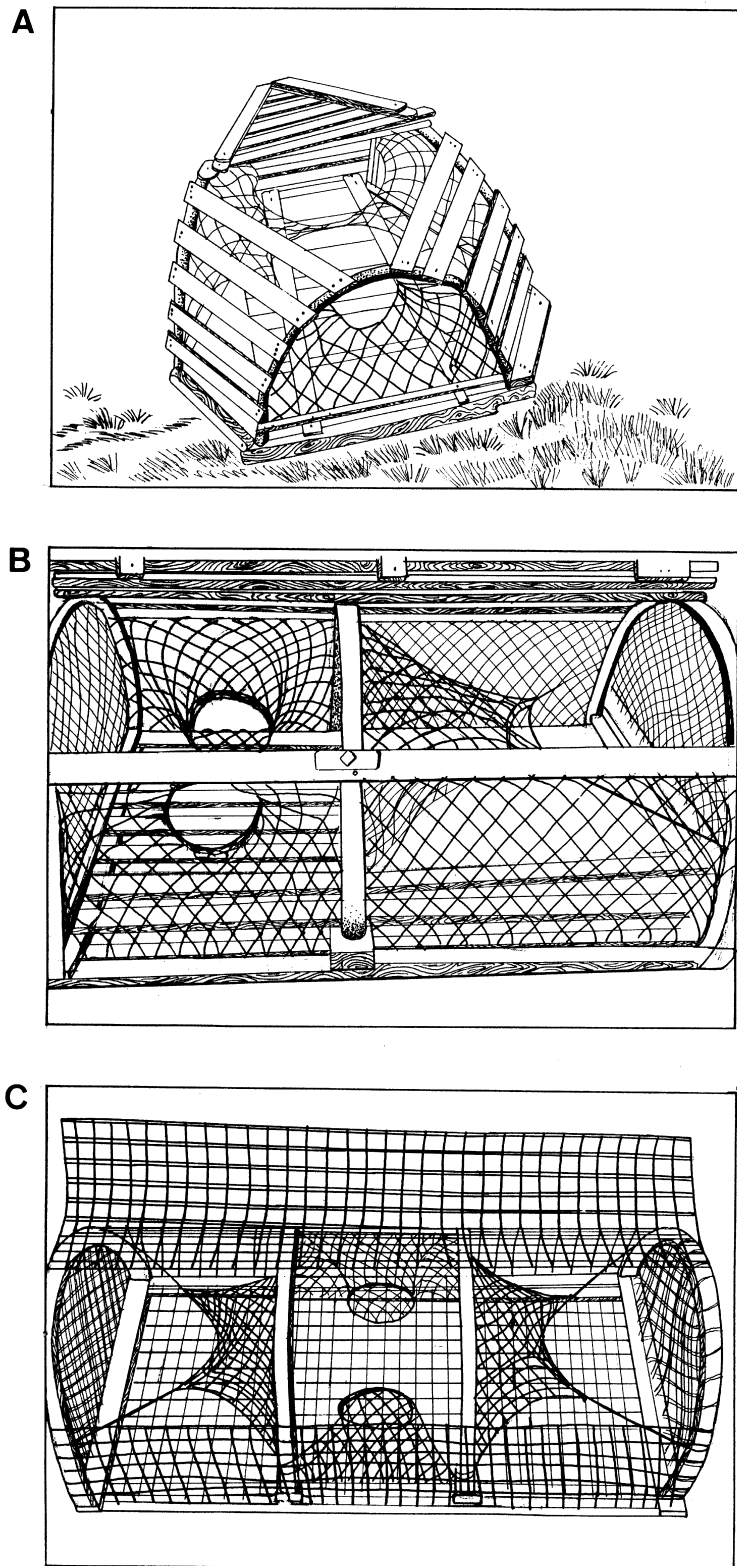


Figure 3.—Types of lobster pots. A) six-sided trap with three entrances and no parlors; B) lath trap with two entrances and one parlor; C) wire trap with two entrances and two parlors. Redrawn from Miller (1995) by Sapphire Tur-Caspar.

Table 1.—Changes in minimum legal sizes, state-by-state, for the American lobster, *Homarus americanus*.¹

Years	Maine			Years	New Hampshire		Years	Massachusetts	
	Total length (inches)	Carapace length (inches)	Maximum length (inches)		Total length (inches)	Carapace length (inches)		Total length (inches)	Carapace length (inches)
1874–1883	10 1/2	(3 5/8) ²		1874–1907	10 1/2	(3 5/8) ²	1874–1907	10 1/2	(3 5/8) ²
1883–1885	9	(3 3/32)		1907–1933	9	(3 3/32)	1907–1933	9	(3 3/32)
1885–1889	10 1/2	(3 5/8)		1933–1941	(9 7/32)	3 3/16	1933–1941	(9 7/32)	3 3/16
1889–1895	9 ³ to 10 1/2	(3 3/32 to 35/8)		1941–1988	(9 1/16)	3 1/8	1941–1950	(9 1/16)	3 1/8
1895–1907	10 1/2	(3 5/8)		1988–1989	(9 11/32)	3 7/32	1950–1988	(9 1/16)	3 3/16
1907–1919	10 1/2	(3 5/8)		1989–1993	(9 7/16)	3 1/4	1952–1989	(9 11/32)	3 7/32
1919–1933	(10 1/8)	3 1/2					1989–1993	(9 7/16)	3 1/4
1933–1935	(8 7/8)	3 1/16	4 3/4						
1935–1942	(8 7/8)	3 1/16	5						
1942–1958	(9 1/16)	3 1/8	5						
1958–1960	(9 7/32)	3 3/16	5 3/16						
1960–1988	(9 7/32)	3 3/16	5						
1988–1989	(9 11/32)	3 7/32							
1989–1993	(9 7/16)	3 1/4	5						

Years	Rhode Island		Years	Connecticut		Years	New York	
	Total length (inches)	Carapace length (inches)		Total length (inches)	Carapace length (inches)		Total length (inches)	Carapace length (inches)
1874–1880	10	(3 5/8)	1874–1875	10	(3 15/32)	1874–1893	10 1/2	(3 5/8)
1880–1895	10 1/2	(3 5/8)	1875–1878	8	(2 3/4)	1893–1935	9	(3 3/32)
1895–1909	9	(3 3/32)	1878–1895	6	(2 1/16)	1935–1941	(9 7/32)	3 3/16
1909–1936	4 1/8 (TBSL) ⁴	(3 1/8)	1895–1909	9	(3 3/32)	1941–1952	(9 1/16)	3 1/8
1936–1966	(9 7/32)	3 3/16	1909–1925	4 1/8 (TBSL) ⁴	(3 1/8)	1952–1989	(9 7/32)	3 3/16
1966–1989	(9 11/32)	3 7/32	1925–1955	(9 7/32)	3 3/16	1989–1990	(9 11/32)	3 7/32
1989–1993	(9 7/16)	3 1/4	1959–1988	(8 7/8)	3 1/16	1990–1993	(9 7/16)	3 1/4
			1988–1989	(9 11/32)	3 7/32			
			1989–1993	(9 7/16)	3 1/4			

¹ Sources:

Kelly (1990).

K. H. Kelly, Maine Department of Marine Resources, West Boothbay Harbor, Maine 04575. Personal commun. 16 Sept. 1992.

Steven X. Cadrin, Massachusetts State Division of Marine Fisheries, Sandwich, Mass. Personal commun. 16 Dec. 1991.

J. I. Nelson, State of New Hampshire Fish & Game Department, Durham, N.H., State of N.H. Fish & Wildlife Documents and personal commun. 5 Feb. 1992.

Thomas E. Angell, Rhode Island Division of Fish & Wildlife, Coastal Fisheries Laboratory, 1231 Succotash Road, RR#1, Wakefield, R.I. 02879. Personal commun. 14 May 1992.

P. T. Briggs, New York State Department of Environmental Conservation, Stony Brook, N.Y. Personal commun. 18 Dec. 1991.

Public Acts of Connecticut, 1874–1971; Public and Special Acts of the State of Connecticut, 1971–1993

² Numbers in parentheses are approximate equivalent measures.

³ 9" was established for lobsters to be canned.

⁴ TBSL = total back shell length from tip of rostrum to center rear of carapace.

prohibited nonresidents from fishing in local waters without permission (Rathbun, 1886). Maine followed suit in 1823, requiring nonresidents to obtain a permit to fish for lobsters (Dow, 1949; Kelly, 1990). Later, Maine enacted a law in 1872 prohibiting the catching, buying, or selling of “berried” lobsters. This was repealed in 1874, and a closed season was established on all lobsters from 1 August to 15 October of each year (Dow, 1949). From 1917, ovigerous females could be sold only to the state, which marked them with a hole punched into their uropod and then released them back into local waters as property of the state (Miller, 1995). In 1948, the uropod punch was replaced by the V-notch (Miller, 1995). In Canada, the holding, buying, or selling of berried females or recently molted lobsters was prohibited in 1873. In 1874, the prohi-

bition on holding, buying, and selling recently molted lobsters was replaced by a closed season (Miller, 1995).

In 1873, the first minimum size limits (76–95 mm carapace length (CL)) were established for landed lobsters in Canada; however, these size limits varied from region to region and continue to do so today. Several U.S. states followed suit in 1874 with a size limit of 10.5 inches total length ((TL) exclusive of claws and antennae) being enacted in Maine, Massachusetts (Wheildon, 1874), New Hampshire, Rhode Island, and New York (Table 1). Connecticut enacted a smaller size limit of 10 inches TL (Wheildon, 1874). These sizes of 10 and 10.5 inches TL are roughly equivalent to 87.8 and 92.3 mm CL, respectively, which is the preferred measurement today. (Table 2 gives conversions of TL to CL.) Smaller sizes

were permitted for cannery lobsters until 1891 in the United States (primarily Maine) (Kelly, 1992; Miller, 1995). In contrast, cannery lobsters continue to be smaller throughout Canada, where the canning industry has had considerably more influence (Miller, 1995).

The average size of lobsters marketed in 1880 was about 92.3 mm CL (10.5 inches TL) in Portland, Maine, and New Haven, Conn.; 96.8 to 101.2 mm CL (11 to 11.5 inches TL) in Boston, Mass.; and 92.3 to 132.5 mm CL (10.5 to 15 inches TL) in New York City (Rathbun, 1884a). In weight, these lobsters ranged from 648.6 g (1.43 lb) at 92.3 mm CL to 1,941 g (4.28 lb) at 132.5 mm CL (Table 2).

Since annual U.S. landings increased significantly from 7,223 metric tons (t) in 1880 to 13,958 t in 1889 (Anderson and Peterson, 1953) (Fig. 4), the estab-

ishment of a minimum legal size was credited with the arrest of the declining supply of lobsters (Rathbun, 1884b). However, even though a size limit of 87.8 mm CL (10 inches TL) to 92.3

mm CL (10.5 inches TL) remained in effect for at least 15 years, these larger lobsters did not actually maintain the lobster stocks. Landings in the New England states alone declined more than

3,175 t or 23% between 1889 and 1892 (Smith, 1898) (Fig. 5), and the average size of landed lobsters decreased. Consequently, around 1893–95 New York, Connecticut, and Rhode Island reduced their size limits to 78.9 mm (9 inches TL), 65.5 mm CL (7.5 inches TL), and 87.8 mm CL (10 inches TL), respectively (Table 1), because smaller lobsters were more abundant. Similarly, landings in the Canadian provinces grew until 1886 and then began a decline, with minor upturns in the late 1890's, 1930's, and 1950's. In the 1980's, landings again began to increase (Miller, 1995) (Fig. 4). Because of these intense fishing pressures which removed the stock of larger lobsters considerably faster than reproduction and natural growth could replenish it, questions arose concerning the age at which sexual maturity was reached and the egg production of mature lobsters.

Herrick (1894), working at Woods Hole, Mass., dissected over 100 females and determined that most reached maturity between 69.9 and 105.7 mm CL (8–12 inches TL). He further determined that the majority would reach maturity by 87.8 mm CL (10 inches TL). He estimated that a lobster of 69.9 mm CL averaged about 5,448 eggs, one of 78.9 mm CL averaged 8,179 eggs, one of 87.8 mm CL averaged 11,705 eggs, and one of 105.7 mm CL averaged 21,810 eggs (Table 2). To date, Herrick's maturity and fecundity findings have been generally confirmed by various researchers in Maine, Massachusetts, and New York (Krouse, 1973; Briggs and Mushacke, 1979; Estrella and McKieran, 1989; Estrella and Cadrin, 1990; Graulich¹).

Herrick (1894) also concluded that all states with size limits less than 92.3 mm CL needed to raise their legal limits, but it was not until 1907 that any state responded. Maine raised its size limit to 95.3 mm CL (10 27/32 inches TL), New Hampshire and Massachusetts lowered their size limits to 78.9 mm CL (9 inches TL), and in Rhode Island, Connecticut, and New York size

Table 2.—Conversion of total length measurements to carapace length measurements with corresponding egg production approximations and weights.

TL (inches)	Conversion of TL to CL ¹		Egg production ²		Weight ³	
	TL (mm)	CL (inches)	CL (mm)	(Approx. eggs)	Pounds	Grams
6	152.4	2 1/16	52.1		0.25	113.9
7 1/2	190.5	2 19/32	65.5	4,269	0.50	226.8
8	203.4	2 3/4	69.9	5,448	0.61	276.7
8 7/8	225.4	3 1/16	77.8	7,802	0.85	385.6
9	228.6	3 3/32	78.9	8,179	0.89	403.7
9 1/16	230.2	3 1/8	79.4	8,354	0.90	408.2
9 7/32	235.0	3 3/16	81.0	8,932	0.96	435.5
9 11/32	237.0	3 7/32	81.8	9,231	0.99	449.1
9 7/16	239.2	3 1/4	82.6	9,537	1.02	462.7
9 1/2	241.2	3 9/32	83.3	9,811	1.04	471.7
9 19/32	243.4	3 5/16	84.1	10,131	1.07	485.4
10	254.0	3 15/32	87.8	11,705	1.23	558.0
10 1/8	257.1	3 1/2	88.9	12,204	1.27	577.1
10 1/2	266.7	3 5/8	92.3	15,841	1.43	648.6
10 27/32	275.4	3 3/4	95.3	13,409	1.57	712.2
12	304.8	4 5/32	105.7	21,810	2.15	975.2
14 13/32	365.4	5	127.0	40,372	3.76	1,705.5
15	381.0	5 7/32	132.5	46,541	4.28	1,941.4

¹ TL = 2.8424 CL + 4.3922, r² = 0.9906, n = 431, from Steven X. Cadrin, Massachusetts State Division of Marine Fisheries, Sandwich, Mass. Personal commun. 16 Dec. 1991.

² Herrick's (1894) calculation: Log₁₀(Fecundity) = -2.4505 + 3.3542 Log₁₀(CL), from Saila et al. (1969).

³ Weight = $\frac{(\text{Length})^{3.0374}}{452} * 0.000692$ from Thomas B. Hoopes, Division of Marine Fisheries, Salem, Mass. Personal commun. 18 Dec. 1991.

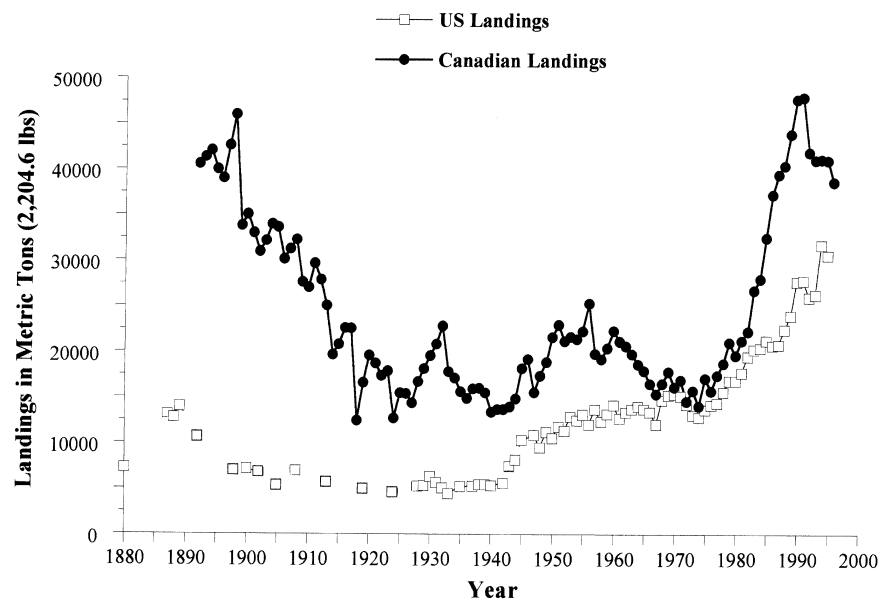


Figure 4.—U.S. and Canadian landings of lobsters (in metric tons) for the years 1880 to 1992. All data from 1976 to 1995 are from preliminary reports of state agencies. Data for 1995 for the U.S. and for 1996 from Canada are preliminary. (U.S. landings from Historical Fishery Statistics Summary of American Lobster Landings, Northeast Fisheries Center, MA, transmitted from R.L. Shultz; Canadian landings from Douglas Pezzack, Lobster Biology & Assessment, Dept of Fisheries and Oceans, P.O. Box 550, Halifax, Nova Scotia B3J 2S7, Canada. Personal commun. 21 April 1997).

¹ Graulich, H. A. 1991. American lobster investigations in New York waters. U.S. Dep. Commer., NOAA, NMFS Compl. Rep., Proj. 3- IJ-11 under Interjuris. Fish Act, 21 p.

limits remained the same at 78.9 mm CL (Table 1).

Herrick (1898) further concluded that laws should be established to prohibit the taking of egg-bearing females. However, despite all states enacting such a law by the turn of the century (Carlson, 1955), annual landings continued to decline. U.S. landings declined from 13,958 t in 1889 to 5,227 t in 1905 and to about 4,407 t in 1924 (Anderson and Peterson, 1953) (Fig. 4), while in Canada a much larger decline was evident, decreasing from 47,620 t in 1886 to 31,746 t in 1906 and then dramatically to 12,200 t in 1924 (Pringle et al., 1993). The European *H. gammarus* fisheries also experienced similar declines (Herrick, 1911a; Bennett, 1980). Table 1 provides the changes in size limits throughout successive years for the various U.S. states.

Combined landings from all states (Fig. 4) were used to interpret the overall condition of the U.S. lobster fishery. However, because Maine landings represented about 50% or more of the catch landed each year (Fig. 5), the use of combined data could result in misinterpretations about declines and/or increases in landings. For example, Figure 4 illustrates a continuous decline in the overall U.S. landings from 1889 to about 1935; however, Figure 5 depicts each state separately and shows that only Maine landings declined, while landings in the other states remained stable or increased. During this period of reduced landings in Maine, the legislature passed what came to be known as a “poverty gauge” of 4 3/4-inch backshell length (slightly longer than CL) in 1907. In response fishermen were thought to routinely land illegal lobsters for home consumption or illicit shipping and to smash undersized lobsters for bait (Acheson, 1997). The legislature then changed the size limit to 3.5-inch CL in 1919, but this did not appreciably raise the landings nor decrease the violations of the law. Finally, after a closure of the fishery along the central Maine coast in the 1920’s and a further reduction of the minimum size limit to 77.8 mm CL (approx. 3 1/16-inch CL), Maine put in place a maximum carapace measure of 121 mm

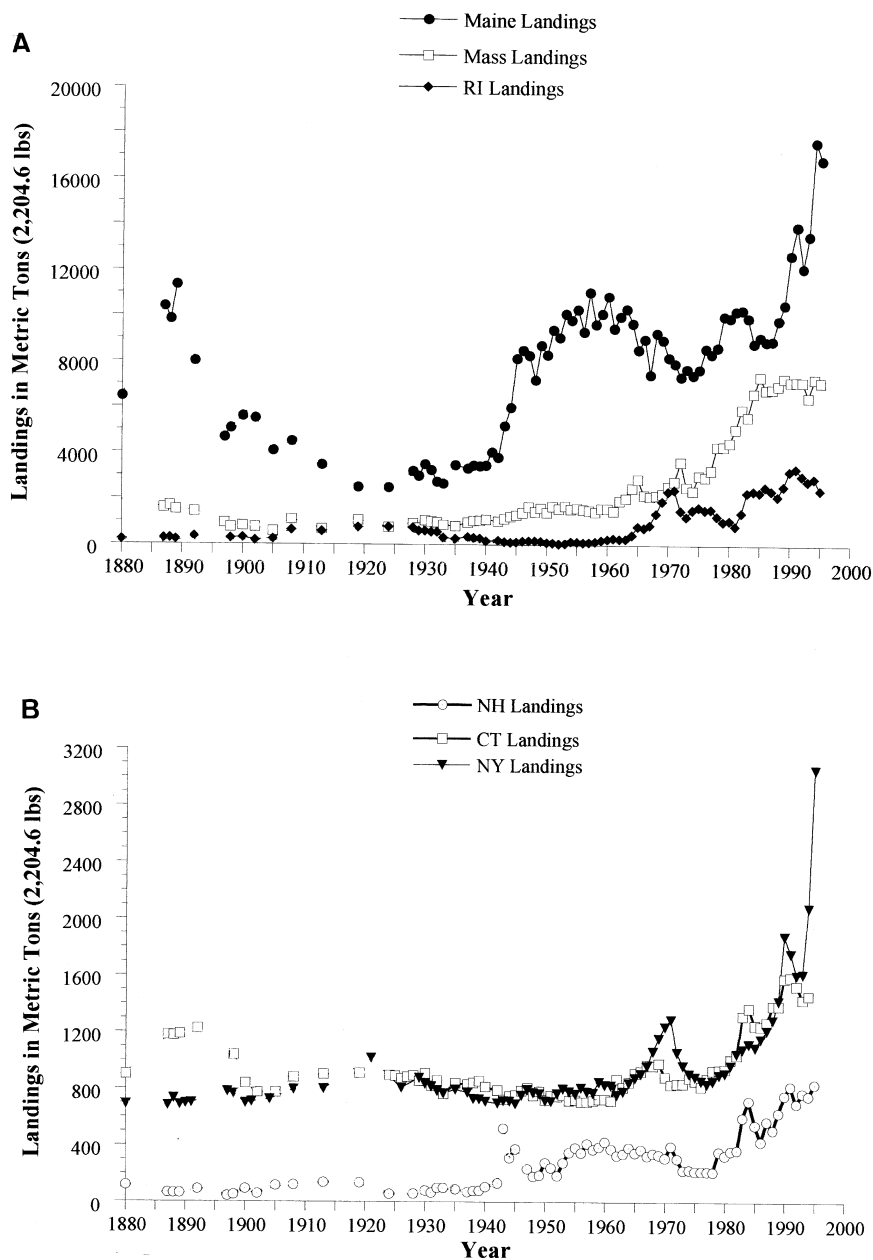


Figure 5.—State-by-state landings of lobsters (in metric tons) for the years 1880 to 1992. A) Landings from Maine, Massachusetts, and Rhode Island; B) Landings from New Hampshire, Connecticut, and New York. Some data points are missing until 1942 and data from 1995 are preliminary.

CL (4 3/4-inch CL) in 1933 (Acheson, 1997). Beginning in 1935 overall landings increased both in terms of total pounds landed and in terms of pounds landed per pot fished (Fig. 5; Table 3). Acheson and Steneck (1997) further discuss a series of hypotheses to

explain the so-called “bust” in the early 20th century Maine fishery.

Environmental Factors and Landing Fluctuations

Insufficient information on the causes of natural fluctuations in landings brought

Table 3.—Historical landing data for the State of Maine, including number of pounds landed, number of pots fished, minimum sizes in effect, approximate weights of lobsters landed, and calculated number of lobsters landed per pot.

Item	1897	1942	1992
Number of pounds landed	10,300,000 ¹	8,400,000 ¹	26,830,000 ²
Number of pots fished	234,000 ¹	187,000 ¹	2,000,000 ²
Number of pounds per pot fished	44	45	13.4
Number of lobsters per pot	31	53	13
Minimum size (mm CL)	92.3	77.8	82.5
Approximate weight (in lbs.) of lobster of minimum size	1.43 ¹	0.85 ¹	1.02 ¹
Average weight (in lbs.) of lobster landed	2.63 ³	1	1.24 ²
Corrected number of lobsters per pot based on average weight landed	16.7	45	10.8

¹ Source: Dow et al. (1975).

² Source: Jay Krouse, Department of Marine Resources, Marine Resources Laboratory, McKown Point, West Boothbay Harbor, Maine 04575. Personal commun. 22 March 1994.

³ Estimate based on the average lobster marketed in 1880, from Rathbun (1884b).

new research efforts, directed at the significant role that environmental factors played in regulating and controlling the survival, size at maturation, catchability, and, ultimately, the supply of lobsters. These factors include, but are not limited to, food, light, salinity, disease, mutilation, social environment, and water quality (Herrick, 1911a; Templeman, 1933, 1936; Aiken, 1980; Aiken and Waddy, 1986; Ennis, 1986a).

Although each of these factors is important, many have postulated that temperature plays a key role in increasing survival of the larvae and post-larvae, accelerating growth rates, and increasing both activity and catchability. Temperature affects larval lobsters throughout their course of development (Hadley, 1906a; Templeman, 1936), shortening their developmental rates when elevated, and increasing their chances of survival (Templeman, 1936; Hughes and Mattheissen, 1962, 1967; Caddy, 1979; Harding et al., 1983; Ennis, 1986a; Mackenzie, 1988; Corey²). Therefore, the number of larvae surviving to settle is more dependent upon favorable environmental conditions than on the number or size of spawning adults (Carlson, 1955). Herrick (1895) remarked that the destruction of a few hundred thousand eggs, or even millions, would not appreciably affect the supply of lobsters at any given point along the coast. If Herrick was correct, then any increase in egg production within the same order of magnitude would not appreciably improve recruitment into the fishery. In fact, when larger lobsters predom-

² Corey, S. 1963. Research on lobster larvae (*Homarus americanus*). Biol. Sta., St. Andrews, N.B., Can. Unpubl. manusc., 16 p.

inated between 1874–1892, landings declined (Smith, 1898; Fig. 5), suggesting that increased egg production was indeed irrelevant. However, Fogarty (1995) suggests that small changes (such as an increase of 1%) in larval survival could dramatically increase the number of lobsters eventually recruiting to the fishery. Nonetheless, recent attempts to explain the low landings in Maine in the 1930's and the higher landings of the 1990's, showed little relationship between landings and temperature, particularly during the recent, so-called, "boom" years (Acheson and Steneck, 1997). Thus, while temperature may improve larval survival, its positive effects on subsequent survival and recruitment to the fishery are uncoupled at some point. This uncoupling has led to the idea that there may be bottlenecks present in the life cycle of the lobster that limit lobster numbers (Wahle and Steneck, 1991).

Elevated summer water temperatures not only accelerate growth rates, they can also induce early maturation (Aiken, 1980; Waddy and Aiken, 1991). Typically, male lobsters mature at the relatively smaller sizes of 50–70 mm CL in most areas, regardless of water temperature (Krouse, 1973; Briggs and Muschacke, 1979). In contrast, there is a wide variation in maturation among females in various geographical locations. For example, higher water temperatures in Long Island Sound, N.Y., Buzzards Bay, Mass., and the Gulf of St. Lawrence, Can., cause females to mature at the smaller size of 60 mm CL, with most maturing at 80 mm CL. In the colder waters of the Gulf of Maine or southern Nova Scotia, females may

not begin to mature until they attain a size of 80 mm CL or larger (Krouse, 1973; Aiken, 1980; Aiken and Waddy, 1980; Waddy and Aiken, 1991). Temperatures also affect the proportion of prerecruits entering (molting) into the fishery (Campbell, 1983; Estrella and Cadrin, 1991). Furthermore, activity and catchability are associated with increased water temperatures (McCleese and Wilder, 1958; Dow, 1966; Flowers and Saila, 1972), which directly affect landings (Taylor et al., 1957; Dow, 1961, 1977, 1978, 1980; Fogarty, 1988; Estrella and Cadrin, 1991; Kelly, 1992, 1993).

Despite the upward trend in landings beginning in the late 1930's, researchers predicted that climatological conditions for the remainder of the century would not improve or maintain the extant landings (Dow, 1980). Furthermore, extant levels of fishing were assumed to be substantially greater than those which would allow the greatest productivity from the resource (Northeast Marine Fisheries Board, 1978). This information caused concern for the long-term viability of the overall fishery with respect to stock and recruitment. Efforts were directed toward unified management and eventually resulted in the establishment of the American Lobster Fishery Management Plan (FMP) in 1983. The FMP was designed to 1) promote conservation, 2) reduce the possibility of recruitment failure, and 3) allow full utilization of the resource by the U.S. fishing industry. The main objective, however, was to support and promote the development and implementation, on a continuing basis, of a unified, regional management program for American lobsters (Anonymous, 1983a).

Recommendations included a uniform size limit of 81 mm CL (3 3/16-inch CL) to be established in all U.S. areas by 1981 (Northeast Marine Fisheries Board, 1978). This size limit was finally implemented in 1985 (Anonymous, 1983a, b). The objective behind the increase in minimum size stemmed from studies of instantaneous mortality rates (fishing and natural), together with fecundity studies, general growth rates (from various areas), and yield

per recruit (Herrick, 1895; Saila et al., 1969; Skud and Perkins, 1969; Krouse, 1973; Briggs, 1975; Uzmann et al., 1977). However, the most important result of those studies was to determine the size at which females reached maturity (Northeast Marine Fisheries Board, 1978).

Fishery Management: The Federal Government and the States

The National Marine Fisheries Service (NMFS) and the U.S. lobster producing states came together in 1978 to formulate a State-Federal Fishery Management Plan (FMP) for the lobster that would provide for a single, unified approach to managing the fishery. The goals of this plan were to adjust minimum size limits appropriately, reduce incidental lobster injury and mortality during fishing, establish the use of escape vents, prohibit possession of ovigerous females, standardize gear marking, and license dealers by state and fishermen by state and/or state and Federal waters (Anonymous, 1998). This plan was referred to the New England Fishery Management Council (NEFMC) in late 1978 for inclusion in the Magnuson-Stevens Act, but was not implemented until 1983. At that time, the FMP established a legal size limit of 81 mm CL (3 3/16-inch CL), prohibited the taking of ovigerous females, and required escape vents in all fixed lobster gear. Since its implementation, the FMP has been amended six times. Amendment 1, approved in 1986, standardized gear marking in the offshore fishery. Amendment 2, implemented in 1987, imposed a series of four incremental increases to the minimum fishable size of 0.8 mm CL (1/32-inch CL), effective in January 1988, 1989, 1991, and 1992, with the goal of reaching 84.1 mm CL (3 5/16-inch CL) in 1992 (Anonymous, 1987b, 1998). Amendment 3, implemented in 1990, required the use of biodegradable escape panels in traps to reduce the possibility of ghost fishing by lost traps.

Despite these approved measures, several industry associations, including the Maine and Massachusetts Lobstermen Associations, requested a delay

in any size increase beyond the 82.5 mm (3 1/4-inch) CL size. These groups claimed that these size increases put them at an economic disadvantage with Canadian lobster suppliers who were allowed to take animals 81 mm CL (3 3/16-inch CL) or even smaller in certain regions (Miller, 1995).

Amendment 4 to the FMP was implemented in 1991 and temporarily rescinded the next scheduled size increases, such that all major U.S. lobster-producing states stood at the 82.5 mm CL size limit (Anonymous, 1991d). In 1994 the NEFMC adopted Amendment 5 to the FMP to address the overfished condition of the lobster resource while maintaining the minimum size of fishable lobsters at 82.5 mm CL. This Amendment was required to avoid the next scheduled increase mandated by Amendment 4, which would have changed the minimum size to 84.1 mm CL (Anonymous, 1994). Amendment 5 also provided a definition for overfishing, appointed committees (called Effort Management Teams) for four regional management areas (Gulf of Maine nearshore, southern New England nearshore, mid-Atlantic nearshore, and offshore), limited access to the fishery for 5 years (1995–1999), and proposed closed seasons, closed fishing areas, mandatory data reporting by all active permit holders, and future length increases if deemed necessary (Anonymous, 1994; Miller, 1995). Amendment 6, approved in 1997, addressed gear conflicts. Furthermore, under a separate legislative authority, under the Atlantic Coastal Fisheries Cooperative Management Act (ACFCMA), the Federal government is allowed to suspend lobster fishing within a state's waters if that state is found to be in noncompliance with an affiliated interstate FMP (Miller, 1995).

According to Amendment 5, the Effort Management Teams were required to establish stock rebuilding programs for their respective regions and to present a set of recommendations to the NEFMC by January 1995. The Council was then required to submit a management plan by July 1995 designed to incorporate the recommendations of the management teams into the FMP for lobsters.

The management teams met their deadline; however, the Council failed to meet its deadline due to the objections of the states of Maine, New Hampshire, Rhode Island, and Connecticut to certain measures in the recommended amendment. Because the NMFS requested that all states commit to participation in the amendment's administration and four states refused, NMFS proposed the withdrawal of the FMP in March 1996 stating that the plan would no longer meet the standards set forth in the Magnuson-Stevens Act requiring the prevention of overfishing (Lockhart and Estrella, 1997; Anonymous, 1998). Nonetheless the NMFS did not withdraw the FMP until an effective state management plan was completed to replace it. The Atlantic States Marine Fisheries Commission (ASMFC) proposed such a plan for state waters in July 1996 and the plan was subsequently adopted in 1997. Lobster fishing in Federal waters is now regulated under the provisions of the 1993 Atlantic Coastal Fisheries Cooperative Management Act (ACFCMA).

In October 1996, the Sustainable Fisheries Act (SFA) amended the Magnuson-Stevens Act (MSA) to require that the NMFS identify all overfished resources under the jurisdiction of fishery management councils (the MSA plan for American lobster, however, was withdrawn in 1999). In the case of an overfished resource which occurs predominantly in state jurisdictional waters along the Atlantic seaboard, the ACFCMA provides for the development, implementation, and enforcement of effective interstate conservation management. The lobster was identified as an overfished resource in 1994. The ASMFC approved Amendment 3 to the Interstate Fishery Management Plan for Lobster in late 1997. Amendment 3 adopted an area approach to the management of the lobster fishery (similar to that in Amendment 5 of the withdrawn FMP) with 7 Lobster Conservation Management Teams. It also adopted coastwide management measures such as making it unlawful to possess lobster parts, speared lobsters, ovigerous females, and V-notched females; requiring ghost panels for non-wooden traps;

and limiting the landings of fishermen using nontrap fishing methods to 100 lobsters per day. Additional coastwide measures included implementation of trap tags, designation of individual fisherman's areas of fishing (beyond which they could not fish), new escape vent sizes, and maximum trap sizes. Three of the 7 areas were required to reduce the number of traps fished per fisherman each year with the goal of reaching 800 traps by the year 2000. The inshore Gulf of Maine area (Area 1) also implemented a maximum size gauge of 5 inch CL in January 1999.

NMFS, citing requirements under the Magnuson-Stevens Act to end overfishing, determined that Amendment 3 of ASMFC's plan did not fully address the measures necessary to end overfishing and thus did not provide adequate protection for conservation of the lobster. However, NMFS did note that the ASMFC plan was an excellent beginning for developing a seamless co-management scheme within state and Federal waters. NMFS was concerned that trap reductions were not low enough to significantly reduce fishing effort and that the ASMFC plan did not specify any conservation measures beyond 3 years despite committing to an 8 year schedule. In March 1998, NMFS drafted a series of alternative management approaches in their Draft Environmental Impact Statement (Anonymous, 1998). Public hearings on these measures were held throughout the affected states through May 19, 1998 to obtain fishermen's views on the alternative options for managing the fishery in Federal waters. As per the Sustainable Fisheries Act, NMFS has until June 1999 to adopt a new Federal management plan. In December 1999, Federal authority for managing lobster fishing was transferred from the Magnuson-Stevens Act to the Atlantic Coastal Fisheries Cooperative Management Act (ACFCMA). Nonetheless, many of the measures and prohibitions were carried over (limited access, no taking of berried, v-notched, or lobster parts, minimum sizes, etc.). New measures included fishing gear restrictions, trap tags, management areas, and consultations with ASMFC.

In 1996, gear entanglements with whales, and specifically the endangered right whale, also came to the fore. The number of right whale entanglements occurring annually is unknown. Kraus (1990) estimated that 57% of the known right whale population exhibits scars from entanglement. Generally, fewer than 10 entanglements are reported per year, representing an unknown fraction of the total. Because the right whale population is so low, the potential removal of even one whale per year requires regulatory action pursuant to the Endangered Species Act and Marine Mammal Protection Act (MMPA). In 1997 NMFS implemented an initial series of restrictions under the MMPA or Magnuson Stevens Act for lobster pot and gillnet gear to protect the highly endangered right whale, as well as humpback, fin, and minke whales. These regulations included time/area closures and gear modification requirements. As the take reduction plan evolves, additional restrictions are anticipated to meet mandated MMPA goals.

Size Limits

Increases in the minimum size were considered a major regulatory tool for the lobster fishery for the following reasons: 1) larger size limits protect females so that they are allowed to molt, mate, and spawn at least once prior to being captured, 2) fecundity increases with increasing body size, and 3) higher yields in weight are expected with increased minimum sizes. However, since 1991, no further size increases have taken place and the concern is that the fishery is now relying too heavily on animals one molt away from recruitment into the fishery to provide the future generations of the species. A recent stock assessment for lobster (NEFSC, 1996) noted that during 1983–94 in the Gulf of Maine relative abundance of lobsters increased. But in 1995 relative abundance of recruits decreased while that for prerecruits increased; a similar trend was seen in Georges Bank (NEFSC, 1996). Furthermore, egg production coming from smaller size classes has been steadily increasing since the 1970's such that 60% and 90% of the egg production in the Gulf of Maine and Massa-

chusetts, respectively, now comes from animals within one molt of legal size. In Rhode Island and central and western Long Island Sound, egg production within one molt of legal size is now 95%. If landings rely more and more on newly-recruited lobsters to support the fishery, then the fishery is compressing egg production potential into a narrow size range (the prerecruits). The fear of managers is that the abundance of the prerecruits may fall, and the fishery will be severely affected (Lockhart and Estrella, 1997).

Furthermore, since size increases have been implemented incrementally, and it takes about 6 years for stock size changes (those in the size of the spawning stock and thus in egg production) to affect recruitment, a period of 20–30 years may be necessary before "so called" benefits, or the lack thereof, would be apparent (Ricker stock size-recruitment model, Anonymous, 1987b). However, based on the upward trend in landings since the late 1930's, it would be rather difficult to assess the impact of recent size increases on the fishery. The increase in landings might also be due to highly favorable environmental conditions (e.g. temperature) or a reduction in lobster predators (Anonymous, 1991d; White, 1991; Pezzack, 1992), although, Addison and Fogarty (1992) give an alternate view. However, since temperature also regulates the productivity of predators (Estrella and Cadrin, 1991), generally increasing their numbers when a breeding stock is present, the question of why lobsters were so recently abundant remains a mystery (White, 1991).

The Role of Shelter

Although the American lobster fishery has experienced several fluctuations over the last century of management, two specific incidents stand out. During the early fishery from 1874 to about 1933, the major lobster producing state, Maine, had a larger size limit for lobsters landed than that in effect in other states (Table 1), yet their landings continued to decline. Then from 1933 (excluding a slight decline in the 1970's), landings remained stable or were on an upward trend (Fig. 5).

These landings increased during the period of the taking of smaller-sized lobsters, despite assumptions of low average reproductive potential of the smaller females (and thus fewer potential recruits into the fishery over time), low survival of larvae and benthic settlers, and increased fishing intensity.

Some of this increase in landings may be due to the availability of shelter, which plays a role in the abundance of lobsters, influencing the sizes, number of occupants, density, and survival in lobster populations (Scarratt, 1968; Cobb, 1971; Howard, 1980). Cooper and Uzmann (1980) have documented the use of shelter by lobsters from their postlarval settling stage onward throughout life, and shelter has been described by some as being a limiting factor (Cobb, 1971; Fogarty, 1976; Fogarty and Idoine, 1986; Richards and Cobb, 1986). Artificial reef experiments have supported the theory that shelter is scarce, since lobsters readily occupy reefs in numbers equal to or greater than those on natural grounds (Scarratt, 1968, 1973b; Briggs and Zawacki, 1974; Sheehy, 1976).

Recently, it has been suggested that settling juvenile lobsters are the most habitat-restricted (Hudon, 1987), and a "demographic bottleneck" has been proposed for this phase of life (Wahle and Steneck, 1991). Lobsters must continually find larger shelters as they grow, which subjects them to predation risks that are inversely related to body size (Wahle and Steneck, 1992; Wahle, 1992a). Accordingly, the tight association with shelter during the early phases of life relaxes with an increasing body size, and larger lobsters can be found in the open without shelters, suggesting a decline in the predation rate for inshore lobsters (Wahle and Steneck, 1992).

Nevertheless, lobsters still need and continue to use shelter throughout their entire lives. Shelter provides a place of protection during their vulnerable soft-shelled (molting) condition and for overwintering, and is a prerequisite for mating (Thomas, 1968; Atema et al., 1979; Karnofsky and Price, 1989; Karnofsky et al., 1989a, 1989b, Cowan and Atema, 1990). In naturalistic settings, an average of 70.3% of the lobsters

that occupy shelters will live closely together, as long as they have individual shelter areas (Karnofsky and Price, 1989). Shelter use and the number of shelters used increases a few weeks prior to molting (Karnofsky et al., 1989b), and lobsters may engage in ritualistic agnostic encounters for such shelters (Scrivener, 1971). The premolt condition may cause both the increase in aggression and the increase in shelter use (Tamm and Cobb, 1978; Atema et al., 1979). Thus, the size distribution and/or availability of shelter may have important ecological and evolutionary consequences for the lobster.

European lobster, *H. gammarus*, populations seem to be locally size limited by the shelter characteristics of the substrate (Howard, 1980). Wahle and Steneck (1991) confirmed that such size limitation also exists within juvenile American lobster, *H. americanus*, populations. Steneck (1989) reported that lobster population densities and body size corresponded to shelter availability which was controlled by regional geology. Population densities of 40–90 mm CL sized lobsters increased significantly when additional shelters were placed in the field (Steneck, 1991). However, as lobster densities increased, the proportion of larger lobsters declined, suggesting that larger lobsters move from regions of higher density to lower density (Steneck, 1991).

In addition, Skud (1969b) reported that the size of lobsters occurring in an area reflected the fishing pressure applied to that population. Thus, the removal of large lobsters would also result in populations of smaller individuals, both inshore and offshore. If these smaller individuals are then fished, the number of lobsters landed may increase, although the pounds landed would be less. Table 3 shows that in 1942 when the legal size of lobsters was considerably smaller than that in effect today or 100 years ago, the number of lobsters landed per pot was indeed greater. This suggests that smaller lobsters are, indeed, more abundant than larger lobsters and suggests that studies similar to those by Steneck (1991) should be pursued.

Given those results, the following scenario is hypothesized to explain the

previous and current landings statistics. During the early lobster fishery, larger lobsters were so numerous that crowding occurred (despite their proclivities to disperse) and they dispersed as much as possible, including to the littoral zone in waters so shallow that they were often exposed during low tide. Pots were usually set out to a depth of 36.6 m and captured lobsters that were at least 92.3 mm CL (10.5 inch TL) in size and about 648.6 g (1.43 lb) (Rathbun, 1884b). Increased fishing intensity removed virtually all of the larger lobsters near shore. The availability of these near-shore grounds was further reduced with the development of industrial factories which discharged their wastes directly into the coastal waters (Cook, 1972) and with the development of coastal areas for marinas and homes.

The tremendous decrease in lobster numbers near shore forced fishermen into deeper coastal waters. Because lobsters were either removed from near-shore environments or forced offshore due to environmental degradation, the amount of space and shelter per lobster decreased offshore and, due to dispersal of the larger lobsters as seen by Steneck (1991), the size of lobsters landed began to decrease. Once this situation equalized, populations of smaller lobsters began to increase. This hypothesis is illustrated in Fig. 6a–c showing the increase in the density of lobsters and demonstrating the decrease in the amount of space. The decrease in amount of space corresponds to the findings of Steneck (1991) that lobsters lose their ability to live at higher densities when they get larger and that they are most abundant where they tend to be of smaller size. Furthermore, a shift in size, due to the increase in the minimum legal size limits, may cause larger lobsters to move into deeper offshore habitats (Skud and Perkins, 1969; Steneck³).

While increases in the size limits may force the larger lobsters to disperse more widely, such that fewer are landed

³ Steneck, R. 1989. Ecological considerations on increasing the minimum legal size of lobsters. Univ. Maine, Ira C. Darling Mar. Cent., Walpole, ME 04573. Unpubl. manuscript, 14 p.

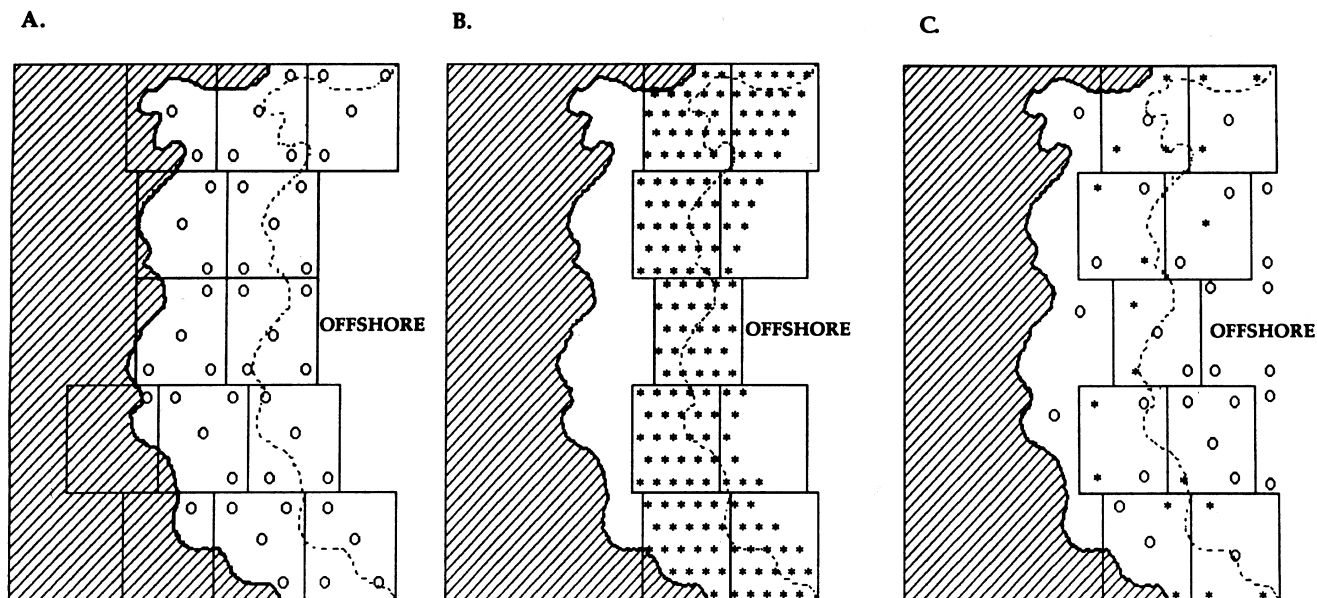


Figure 6.—A) Inshore lobster fishery (ca. 1800's). Larger lobsters (> 90 mm CL) dominated this fishery and were caught close to shore with traps set out to a depth of about 36.6 m (slashed line). Each square represents 10,000 m² and each open circle 10 lobsters of a size > 90 mm CL. B) Inshore lobster fishery (ca. 1930 to 1990). Smaller lobsters (< 90 mm CL) after removal of larger lobsters (> 90 mm CL), due to intense fishing pressure. Smaller lobster densities equalized as a result of decrease in the minimum legal size limit. Each square represents 10,000 m² and each asterisk 200 lobsters of a size < 90 mm CL. Slashed line is the general area where lobstermen set their pots, at a depth of about 36.6 m (121 feet). C) Inshore lobster fishery (ca. 1990 to 1993). As a result of increased size limits, larger lobsters diffuse from regions of high density to those of low density. Likewise, once lobster size changes, lobster density also changes, such that fewer large lobsters live in the same area. Asterisk represents lobsters of a size < 90 mm CL; open circles represent lobsters of a size > 90 mm CL. Slashed line is the general area where lobstermen set their pots, at a depth of about 36.6 m (121 feet).

per pot, intense fishing efforts may remove them quickly. Currently, a minimum size of 82.5 mm CL (3 1/4-inch CL) is in effect for all major lobster-producing states (Table 1). The mean size of lobsters landed has increased to 87.2 mm CL in New York (Briggs, 1992), 88.6 mm CL in Maine (Krouse et al., 1990), and 88.8 mm CL in Massachusetts (Cadrin and Estrella, 1993). These sizes are similar to the 87.8 and 92.3 mm CL minimum sizes in effect in 1889 and 1892, respectively. As in those years, lobster landings declined from 1991 to 1992 by 2,493 t or 9% in the United States (Fig. 4). Removal of the larger lobsters from the fishery over a relatively short period of time, will tend to result in a fishery reliant upon the newly recruited lobsters that might initially be found at higher densities. This could result in a spike in the landings, as was seen in the early 1990's. However, such a reliance on new recruits might present problems if the

abundance of the prerecruits (those one molt away from recruitment) declines for whatever reason (habitat destruction, unfavorable environmental conditions, etc.). If the numbers of those recruiting into the fishery is reduced, then landings would eventually begin to decline. Thus far, the relative abundance of prerecruits has been steady or increasing in most areas (NEFSC, 1996).

Pot loss, which provides shelter where it may already be limiting, may also affect the density of lobsters. Sheldon and Dow (1975) estimated that an average of 20–25% of pots were lost in the Maine lobster fishery annually, and 80% of these pots were capable of “ghost fishing” for an average of 2 years before they become non-functional. However, effective 28 May 1992, traps were required to possess either a ghost panel made from biodegradable material or to have their escape vents attached with a biodegrad-

able clip. These new regulations render the traps nonfunctional in about 1 year (Blott, 1978; Anonymous, 1987b, 1989, 1991d). Once they cannot retain a lobster against its will, they become added shelter. Steneck (1987) reported that removal of pots from a highly populated lobster area resulted in a considerable drop in abundance of lobsters after a 30–45 day period. Dow (1980) reported that scuba divers observed lobsters partially entering traps, consuming the bait, and returning to their burrows. In areas where intensive fishing is conducted, 80% of the lobster's diet may come from baited pots (Steneck, 1987). Furthermore, escape vents used today allow undersized lobsters to enter and leave the pots at will and thereby provide them with food and temporary shelter (Landers and Blake, 1985).

These observations show the influence that pots may have had, and may continue to have, in increasing the abundance of lobsters by providing them

with more shelter and a food source. As further support of this theory, the lobster fishery has utilized the pot to catch lobsters since the mid-19th century (Cobb, 1901; Dow, 1949). If we assume only a 1% loss of pots per year for the overall lobster fishery (instead of the 20–25% quoted for Maine alone), then the number of pots that have been lost over a period of 150 years would have added significantly to the shelter made available for lobsters. A decrease in space inshore and movement of larger lobsters offshore, along with added shelter inshore, could cause a clumping effect where smaller lobsters would live closely together. Such clumping effects have been observed by Karnofsky and Price (1989) and Karnofsky et al. (1989a, b) in both the laboratory and field experiments, respectively. If the above hypothesis holds true, larger size limits for lobsters may have great implications for future inshore landings, as they did in the past. The highest densities of large lobsters (>90 mm CL) reported is 50 per 10,000 m²; that same space can accommodate 5,000 smaller lobsters (<90 mm CL)—a hundredfold increase in the number of animals (Steneck³). Thus, smaller size limits result in the taking of more lobsters since they occur at higher densities and cause landings to increase (Skud, 1969a; Skud and Perkins, 1969; Uzman et al., 1977; Fogarty et al., 1982). Clearly more research is needed to establish estimates of minimum and maximum densities for variously sized lobsters, with respect to the amount of space they require and the habitat limitations they face.

For comprehensive reviews on other protective measures and regulations for the management of both *H. americanus* and *H. gammarus* lobster fisheries see Herrick (1911a), Bennett (1980), Cobb and Phillips (1980), and Cobb and Wang (1985). For emphasis on the American lobster fishery see Anonymous (1983a, b; 1986, 1987b, 1989, 1991d), MacKenzie and Moring (1985), and Northeast Marine Fisheries Board (1978). For specific reviews on regulations during the course of their development in Canada and Maine see Wilder (1965), Pringle et al. (1983), Kelly

(1990), Pringle and Burke (1993), and Miller (1995).

The Development of Artificial Propagation

Despite stringent laws prohibiting the landing of “berried” lobsters in both Canada and the United States, a significant number of females with eggs were scrubbed (eggs removed) and sent to canning factories or to market (Herrick, 1895, 1911a; Smith, 1898; Anonymous, 1906; Wilder, 1954, 1965). This frequent sacrifice of eggs was believed to be a major contributing factor in the lobster decline in the late 1800’s. Consequently, artificial propagation (culture) of lobsters was seen as a way to reverse the loss of the millions of eggs destroyed by scrubbing. The eggs saved could be hatched and released to preserve, or possibly increase, the supply of lobsters (Moquin-Tandon and Soubeiran, 1865; Wood, 1869; Sars, 1879; Ryder, 1886a; Rathbun, 1892; Herrick, 1894, 1895; Bowers, 1900; Bumpus, 1901b; Mead and Williams, 1903; Herrick, 1911a; Scattergood, 1949b; Wilder, 1965). Various culture methods were employed, some of which approximated the natural conditions of tidal ponds and man-made (enclosed) basins or parks, and others which used carefully controlled laboratory conditions.

Early Work

In 1858, Guillou began culturing experiments with the lobster *H. gammarus* at the laboratory of Concarneau in South Brittany, France (de Maude, 1858, as cited in Latrouite and Lorec, 1991; Latrouite⁴). Adult lobsters were maintained in natural and man-made fish ponds and/or in tanks in the laboratory. The fish ponds consisted of naturally enclosed basins formed by rocks, occupying an area of about 1,500 m² where the bottom consisted of sand, mud, and rocks. These ponds were divided into six different sizes, made by thick barriers capable of withstanding the pressure of the sea. They had a gate which opened freely to allow the

⁴ Latrouite, D. 1992. Ifremer, Centre de Brest, B.P. 70-29280 Plouzane, France. Personal commun., 24 Jan.

water to renew itself every 12 hours, following the tidal ebb and flow. Lobsters were fed shellfish and fish during confinement (Moquin-Tandon and Soubeiran, 1865).

The Concarneau laboratory had a total of 85 tanks, small and large, where observations were made on lobster hatching, metamorphosis, and behavior. In 1865, Guillou and Coste reared a considerable number of lobsters and recorded their length and weight for Stages IV through XIV, and they were reported by Moquin-Tandon and Soubeiran (1865) to have remarked, “we may hope that it will be possible to regenerate the fishery on parts of our coast.” Guillou and Coste noted that the rearing of lobster larvae was technically easy, which led to the idea of “reseeded” and enhancing the waters (Latrouite⁴).

Lobster Parks

Because of the successes in France, the establishment of similar operations in the United States for *H. americanus* was recommended (Wood, 1869). Two “parks” were established: one in Massachusetts in 1872 and the other in Maine around 1879 (Rathbun, 1886). According to Smith (1898), “parking” involved retaining egg-bearing female lobsters in natural, enclosed basins where they were allowed to hatch their eggs. This form of culture was also used in Stavanger, Norway, in 1873–75 and in Canada around 1903 (Corrivault and Tremblay, 1948, cited in Scattergood, 1949b). In Norway, man-made enclosures (parks) in the natural environment were built, and egg-bearing lobsters, *H. gammarus*, were placed inside cork boxes about 1.5 m square × 0.6 m deep within the enclosures. Lobsters were successfully hatched and reared through their larval stages until they reached Stage IV or V when they exhibited a crawling habit (reported by Rasch, 1875; Sars, 1879). Appelløf (1909a) also conducted lobster park experiments in 1892, with limited success in Kvitsøy, Norway. Despite these early successful efforts, it was soon determined that this form of natural larval culture was not an efficient way to replenish the supply of lobsters; therefore, these experiments were

discontinued (Smith, 1898; Bowers, 1900; Appelløf 1909a; Corriveau and Tremblay, 1948, cited in Scattergood, 1949b).

Hatching Jars

Meanwhile other researchers actually hatched lobster eggs in jars. In Scotland, Saville-Kent (1884) hatched the eggs of *H. gammarus* and kept the larvae in small jars where they were maintained and fed with minced fish, and their water was changed every day. He reared lobsters to the size of 1 inch, or about Stage V–VI, when they would hide upon release onto rocky grounds (reported in Williamson, 1905, and Herrick, 1911a). That same year (1883), the Norwegian G. M. Dannevig, began experimenting with hatching of “detached eggs.” He successfully hatched the eggs, but the lobsters experienced high mortality after the first larval stage. This mortality was attributed to disease and/or cannibalism (Dannevig, 1885a, cited in Scattergood, 1949b). Dannevig continued his work, and in 1885 he reared about 200 lobsters through the first three larval stages, with a survival rate of around 47% (Dannevig, 1885b). Several of these lobsters were held and reared for 9 weeks while being fed on the soft parts of crabs. They molted five times, measured 21 mm (total length) on Stage V, and were of a greenish-gray color (Dannevig, 1885c).

McDonald Jars

In 1883, a seaside laboratory was set up at Woods Hole, Mass., by the U.S. Commission of Fish and Fisheries (Smith, 1908), where small quantities of *H. americanus* lobster eggs were successfully hatched. However, large-scale artificial propagation did not begin until 1886, after completion of the new laboratory in 1885 with flowing seawater (Rathbun, 1892; Bowers, 1900). In 1886, experiments progressed so well that millions of eggs were detached from female lobsters and hatched in McDonald hatching jars. The McDonald hatching jar (Fig. 7) gave the best survival—as high as 93% from egg to the first stage larvae (Smith, 1898; Bowers, 1900). Billions of first stage larvae were hatched and released directly into nearshore waters to ensure a contin-

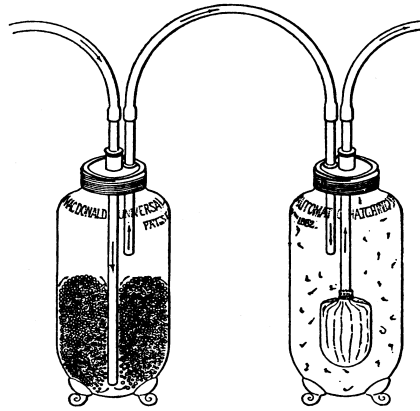


Figure 7.—McDonald Hatching Jar. From McDonald (1883).

uous supply of lobsters in the future (Herrick, 1911a, b; Barnes, 1939). For a full description of the automatic hatching jar (the Downing, Chester, or McDonald hatching jars) and the McDonald tidal box or Nielsen incubator, the reader is referred to McDonald (1883), Brice (1898), Galtsoff (1937), Havinga (1921), and Roché (1898, cited in Scattergood, 1949b).

Scrim Bags

Despite the success of the McDonald jar, the question of larvae survival after release into nearshore waters arose, and Herrick (1894) speculated that not more than 2 in 10,000 larvae survived their pelagic life. Later, other researchers estimated that not more than one-tenth of 1% survived (Mead, 1905; Sherwood, 1905). Therefore, researchers concluded that hatching eggs and liberating the Stage I larvae was not an effective way to replenish or improve the natural supply of lobsters (Dannevig, 1885a, cited in Scattergood, 1949b; Herrick, 1894; Mather, 1894). Instead it was recommended that the larvae be reared to their bottom-crawling (benthic) stage, in an effort to reduce larval mortality that occurred in nature. Mather (1894, 1900) suggested that the larvae be reared individually in a tank or in small compartments. However, he concluded that it would not be possible, at that time, to feed a million or more individually housed lobsters.

In 1898, Bumpus, Mead, and their associates at Woods Hole, Mass., and

at Wickford, R.I., began a series of systematic experiments to find a way to rear postlarvae (Bumpus, 1901b; Barnes, 1906a; Emmel, 1908; Mead, 1910). Many different devices were adapted and tried (e.g. artificial pools, enclosures made of wire screen which were submerged or floating in water, glass jars of various sizes, and huge canvas bags and boxes), but all proved ineffective (Bumpus, 1901b; Sherwood, 1905). However, between 1898 and 1899, Bumpus succeeded in rearing several hundred larvae to Stage IV in scrim bags (bags made of light, loosely woven cotton or linen) at Woods Hole (Mead, 1905, 1910).

Despite this success, the previous failures to rear larvae resulted in the suggestion that environmental conditions at Woods Hole were not ideal for the development of the young lobsters. The same apparatus used at Woods Hole was tested at various other locations (e.g. Annisquam River, Gloucester, Mass.; Orr’s Island, Maine; and Wickford, R.I.) (Bumpus, 1901b; Sherwood, 1905). Based on the results of these experiments (Sherwood, 1905), the other stations were abandoned for the season, and all efforts were transferred to Wickford, R.I., which had the highest water temperatures and the best availability of natural plankton (Bumpus, 1901b; Sherwood, 1905).

Water Agitation

Research was then directed towards the design of an apparatus for keeping the water agitated in the scrim bags so larvae would not settle to the bottom where cannibalism was most prevalent. Originally, paddles were used to stir the water to keep it in constant motion. However, this method was too time consuming because it had to be done manually. In 1901, new equipment was devised, consisting of a two-bladed propeller designed and installed by Sherwood (Mead, 1902, 1910; Fig. 8). This propeller kept the water in constant circulation inside the rearing bags (0.9 m in diameter and 1 m deep), and with this new system 8,974 Stage IV lobsters were successfully reared from eggs that were stripped from females (Sherwood, 1905). The bags were suspended from

frames attached to a floating house-boat (laboratory) directly on the water (Beasley, 1904; Middleton, 1909). Later, the bags were enlarged to 3.6 m² by 1.5 m deep, so that rather than scrubbing eggs, female lobsters could hatch their eggs within crates placed directly into the bags (Barnes, 1906a). The first system is fully described in Mead (1902) and Sherwood (1905), and that of the second system is in Mead and Williams (1903). It should be noted that Mead's "original method" bears some resemblance to Nielsen's floating incubator (Firger, 1974), which may have been modified for Mead's system.

The success of the enlarged bags was evident by the high output of lobsters which followed. By 1920, Wickford's hatchery reached the million mark in rearing Stage IV and some Stage V lobsters (Havinga, 1921, cited in Scattergood, 1949b). The highest production was obtained in 1936, when Wickford reared 1.7 million Stage IV lobsters (Carlson, 1955). In conjunction with rearing Stage IV lobsters, success was also achieved in rearing Stage V lobsters in substantial numbers. The methods were similar to those of rearing Stage IV, and survival rates were estimated to be up to 80%, with an average of 60% to Stage V (Barnes, 1907). Notwithstanding the above success, many future hatcheries were still built upon the idea of hatching eggs and releasing Stage I lobsters.

The Banning Box

In 1929 at the Noank hatchery in Connecticut, Capt. Banning constructed an indoor rearing system, based upon the Norwegian plan (Carlson, 1955), consisting of a hatching trough (Fig. 9) in which female lobsters were held until they hatched out their larvae, and a square wooden box about 400 mm × 400 mm × 350 mm (Fig. 10), into which the larvae were transferred. The latter became known as the "Banning Box" (Dexter, 1986). Circulation in the box was made by introducing water into a circulator containing small holes at the bottom from which fine jets of water emerged in an upward motion. Larvae and food were kept in a constant upward motion (Anonymous, 1930;

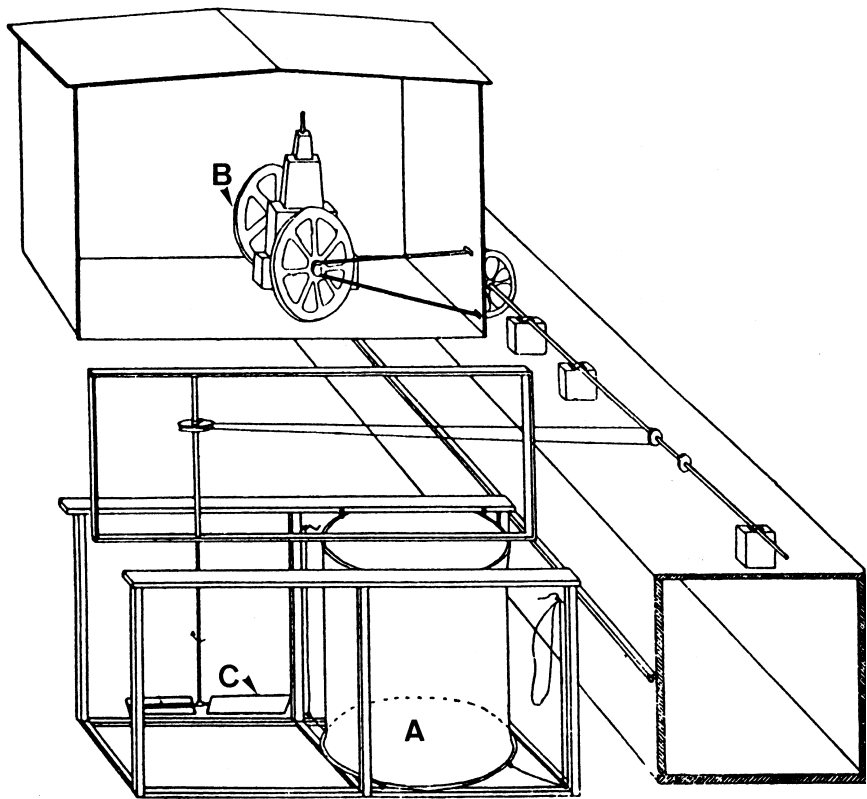


Figure 8.—Agitation unit used at the Wickford, RI hatchery for hatching and rearing larvae. A) scrim bag or car where lobster larvae are contained; B) engine to drive propeller system; C) propeller or fan, 14 inches long × 5 inches wide, made from cypress and screwed into a piece of maple, the other end of which is connected to a tee. (Note: second bag removed to show propeller system.) From Sherwood (1905).

Cobb, 1932). Barnes (1939) (and in Anonymous, 1930) reported that this system was preferable to that used at the Wickford, R.I. hatchery. His conclusion was based on the fact that this system could be used indoors, had greater possibilities of refinement, was less expensive to run, and resulted in higher survival rates of Stage IV lobsters. John Hughes, the first director of the Massachusetts State Lobster Hatchery and Research Station, further refined the Banning Box by replacing the square wooden units with cylindrical, fiberglass pots (350 mm deep, 400 mm in diameter). The square circulators were also replaced by round ones (Fig. 11; Anonymous, 1965).

The Hughes Pot or Kreisel

These refinements resulted in the development of the "Hughes Pot," "plankton-kreisel," or just simply "kreisel" (Hughes

et al., 1974; Fig. 11). The flow pattern of this system resulted in constant turbulence which maintained a homogeneous distribution of the larvae and their food and minimized interactions between larvae that could culminate in cannibalism (Hughes et al. (1974) gives construction and hydraulic characteristics). At densities of 2,000 larvae per kreisel, survival in this system was estimated at 75–85%, with larvae being fed *Artemia salina* brine shrimp (Hughes et al., 1974).

In Helgoland, Germany, Greve (1968) also designed a "planktonkreisel" for culturing and rearing planktonic marine organisms. Unlike the "Hughes Pot," an inside-sand filter arrangement (Fluchter, 1964) was incorporated directly inside the kreisel to provide self-contained filtration of the culture medium (Greve, 1968). Although this system was successful for the culture

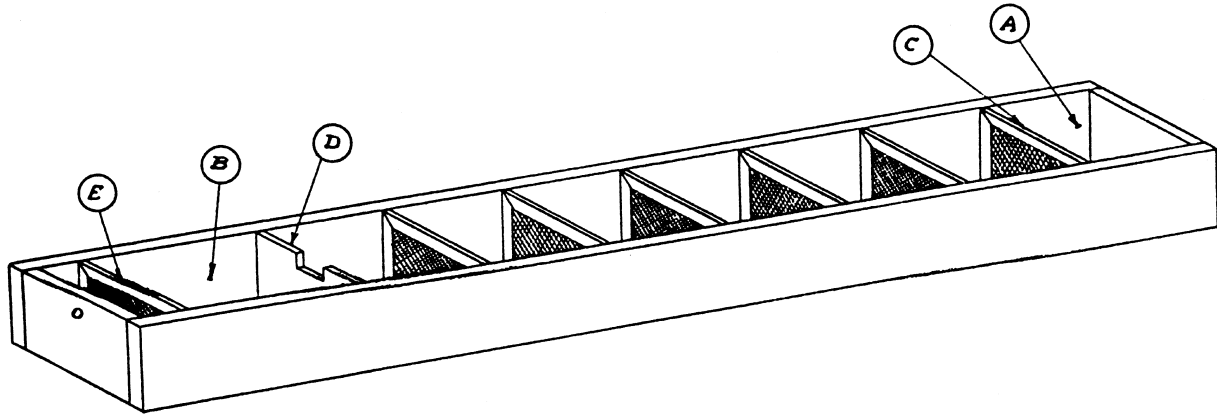


Figure 9.—Hatching trough used at the indoor Connecticut State Hatchery in connection with the Banning Box. The trough is 14 inches (35.56 cm) wide × 8 inches (20.32 cm) deep and consists of 7 compartments (A) which hold female lobsters. Each compartment is separated by a 3/8 inch mesh screen (C) which allows the larvae to pass through. The last compartment's (D) flashboard has its top cut away so that the larvae flow through the opening to the next compartment (B) 20 inches long by 14 inches wide. Larvae are prevented from entering the outflow by the #18 mesh screen (E) at the end of the compartment. All compartments are covered, except for compartment B, which is left open to allow the larvae to display their phototactic responses. From compartment B, the larvae are transferred to the Banning Box. From Anonymous (1930).

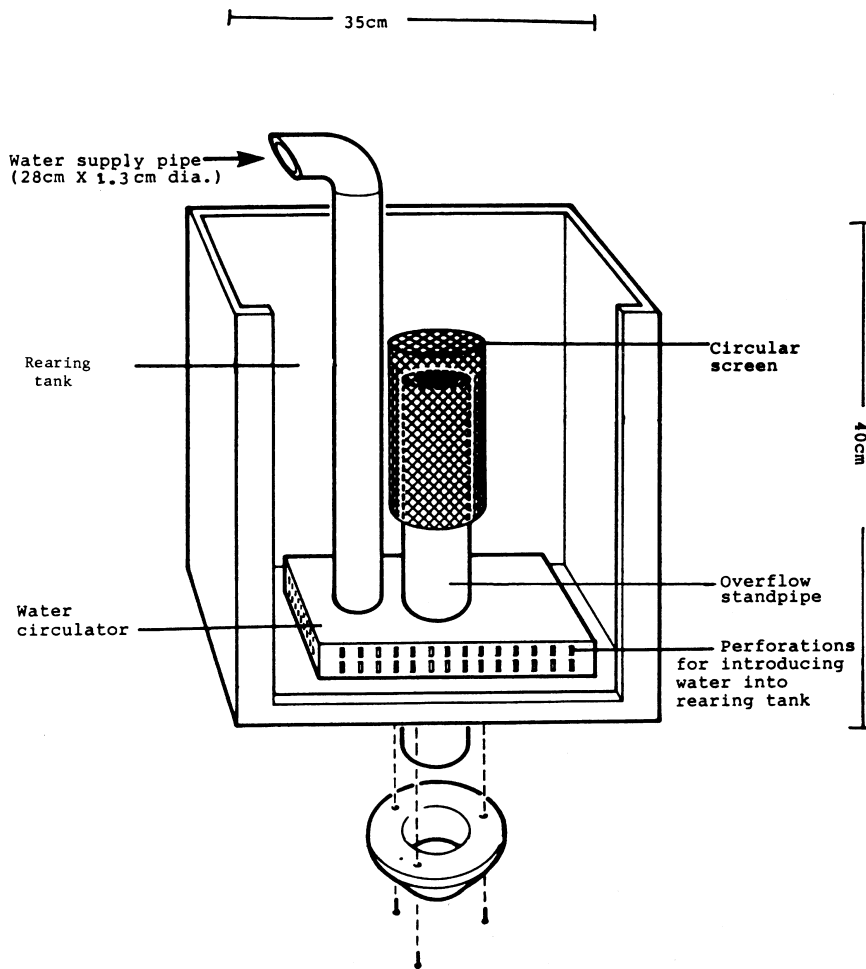


Figure 10.—Banning Box. Redrawn from Anonymous (1930) and Cobb (1932).

and rearing of ctenophores, chaetognaths, and meroplanktonic crustaceans, the "Hughes Pot" became the most popular kreisel for culturing larval lobsters.

Since then, other modifications have been added to the basic kreisel. Serfling, Ford and Van Olst incorporated 16 kreisels into four rearing systems and developed added features of temperature control, filtration (Serfling et al., 1974a; Fig. 12), and automatic feeding devices for the larvae (Serfling et al., 1974b; Fig. 13). Stocked at densities of 4,000 larvae per kreisel and with an average survival rate of 75%, these four rearing systems could yield 48,000 Stage IV lobsters every 10–12 days at temperatures of 22°C (73°F)—in other words, nearly half a million larvae could be produced in about 120 days (Klopfenstein and Klopfenstein, 1974; Serfling et al., 1974a).

Color Morphs

Due to the seeming lack of evidence that hatchery operations (particularly in the case of "seeding" coastal waters with postlarvae) were having a positive effect on lobster landings, researchers began to investigate the use of color morphs of the lobster. Through controlled matings, red, blue, white, orange, and multiple-colored lobsters could be cre-

ated (Anonymous, 1966, 1967; Hughes, 1968a; Shleser, 1971). These oddly colored lobsters are extremely rare in nature, appearing only once in every 15 million lobsters (Syslo, 1986); thus, it was hoped that color morphs could serve as a natural tag through which hatchery efforts could be assessed. Today, this is actually being accomplished (Plante, 1989; Irvine et al.⁵; see also the section Aquaculture Potential: Resource Enhancement), although survival rates of these color morphs has not been assessed, compared to survival of wild type coloration lobsters.

Hatchery Establishment

The success of these early experimental culturing stations resulted in the construction of more than 20 hatcheries in the United States, Canada, Norway, France, and the United Kingdom between the years 1885 and 1954 (Scattergood, 1949b; Carlson, 1954, 1955; Kenslor, 1970; Bardach et al., 1972). In Canada alone, there were 14 such hatcheries in the areas of Bay View, Nova Scotia; the Southern Gulf of St. Lawrence, and on the outer coast of Nova Scotia (Wilder, 1965).

Originally, the purpose of these Federal and state-supported hatcheries was to hatch lobster eggs artificially. During their operations, experiments were conducted to determine both the best methods of hatching the eggs and the best kind of apparatus.

New York Hatcheries

Due to the extremely low lobster populations in New York waters during the late 1880's, lobster propagation was begun in 1886, when Fred Mather, superintendent of the Cold Spring Harbor Fish Hatchery, obtained 50,000 eggs and 5,000 larval lobsters from the U.S. Fish Commission at Woods Hole, Mass. Although all of the eggs died in transit, 4,000 of the larvae survived and were liberated into Cold Spring Harbor (Mather, 1887). By 1891,

⁵ Irvine, C. M., B. Beal, R. C. Bayer, S. Chapman, and D. A. Stubb. 1991. The efficacy of blue colormorphic lobsters in determining the feasibility of hatch release programs. Manuscr. Rep., 16 p. Avail. from The Lobster Inst., Univ. Maine, Orono, ME.

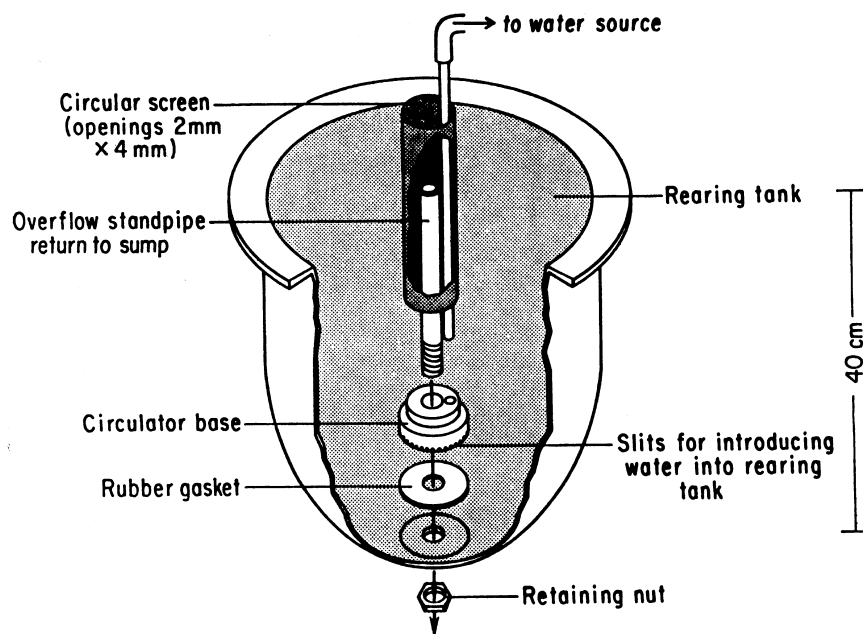


Figure 11.—Hughes Pot or Kreisel. From Hand et al. (1977). Used with permission.

27,700 first stage larvae were successfully hatched (Anonymous, 1892). Egg-bearing females were caught by local lobstermen, and their eggs were hatched in McDonald hatching jars (Anonymous, 1899). In 1900 the Cold Spring Harbor hatchery released 2.4 million larval lobsters (375,000 more than the previous year) into Long Island Sound (Wood, 1901). Despite this success and that of succeeding years in which 2–3 million first stage lobsters were released, this hatchery was discontinued in 1902 due to the lack of a boat for seeding efforts and a dispute between New York and Connecticut over fishing territories (Wood, 1903; Walters, 1904; Anonymous, 1909). Around 1909, an auxiliary hatchery opened at Fort Pond Bay, Montauk, N.Y. Rather than using methods currently in practice, this operation hatched first stage-larvae in floating boxes used for hatching shad (Walters, 1911). In 1910, 7,005,180 first stage larvae were hatched, while in 1911 45,100,000 larvae were hatched (Anonymous, 1912). This hatchery continued operations until 1918 when the state passed a regulation that required officials to purchase egg-bearing females from lobstermen and mark them with

three eyelet holes through their uropods. If these lobsters were later recaptured, they could not be resold (Anonymous, 1919, 1920).

Connecticut Propagation

By an act of the legislature in 1905, Connecticut established a hatchery at Noank where the original purpose was to hatch detached eggs in McDonald hatching jars. In 1906 alone, 20.1 million Stage I larvae were hatched and liberated (Anonymous, 1906). By 1936, the Noank hatchery was using the Banning Box and successfully reared and released over 500,000 Stage IV lobsters into the coastal waters of Connecticut (Carlson, 1955). The hurricane of 1938 destroyed the Noank hatchery, but it reopened in 1940, and continued its operations, rearing in excess of 3 million Stage IV lobsters during 1940–54. Then the Board of Fisheries and Game concluded that hatchery operations were uneconomical and recommended its closure (Anonymous, 1955). Carlson (1955) gives a complete evaluation of the recommendations. When the Noank hatchery was transferred to the University of Connecticut, egg-bearing female lobsters were purchased from

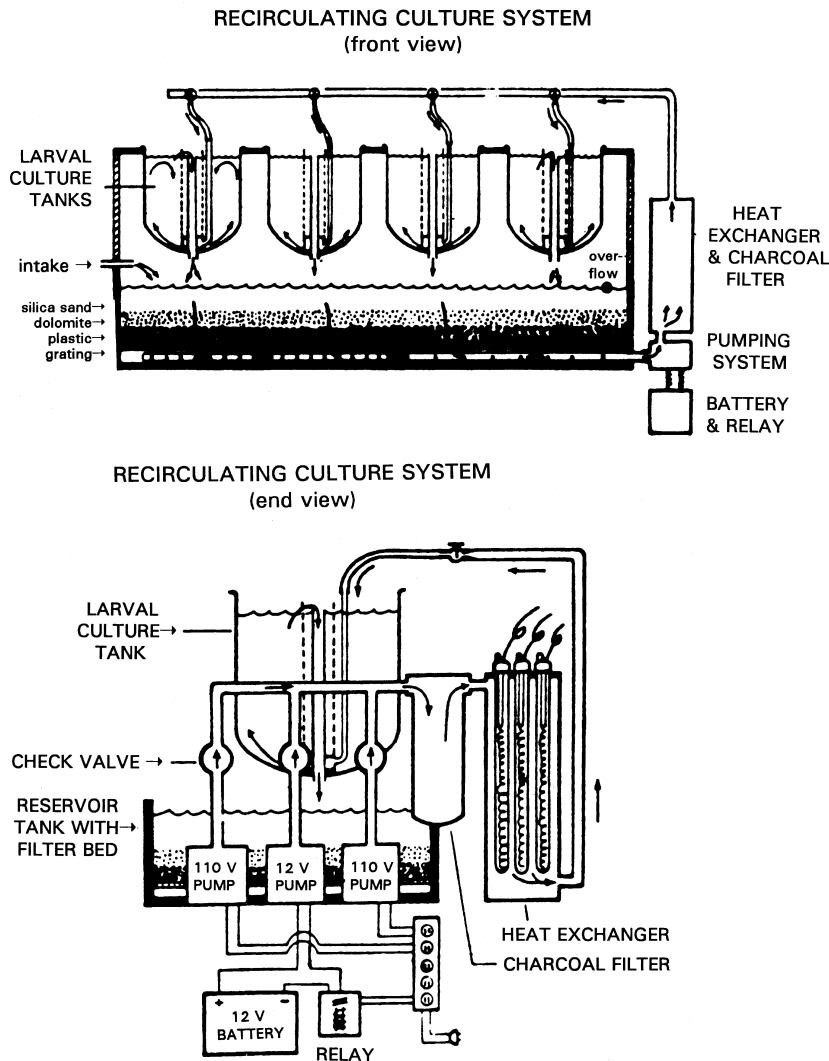


Figure 12.—Recirculating culture system incorporating several kreisels with the added features of temperature control and filtration. From Serfling et al. (1974a). Used with permission.

the lobster fishermen and returned to the state waters as a conservation measure (Anonymous, 1955).

Rhode Island Propagation

The Wickford, R.I. hatchery, which was highly active after the turn of the century, was the site of many of the new efforts to find the most effective rearing technique. By 1920, Wickford's hatchery reached the million mark in rearing Stage IV and some Stage V lobsters in scrim bags with water agitation (Havinga, 1921, cited in Scattergood, 1949b). By 1936, they increased pro-

duction to 1.7 million Stage IV lobsters (Carlson, 1955). Unfortunately, a 1938 hurricane destroyed the hatchery at Wickford, R.I., but it was rebuilt. Another hurricane destroyed the Wickford hatchery again in 1944, but from 1940 through 1943, it hatched, reared, and released into local waters over 5 million Stage IV lobsters. Although lobster rearing ended in 1944 due to the second hurricane, the artificial hatching of eggs continued until 1951 (Carlson, 1955).

In 1989 a large oil spill resulted in a settlement to the state for restoration of

affected species. NMFS approved funds to place six small artificial cobble reefs off Narragansett Bay into which hatchery reared, microwire tagged postlarval lobsters will be seeded onto three reefs, while the other three reefs will be used to make comparisons (Nor'Easter, 1996). These reefs are about 10 × 20 m each, separated by 30 m and were placed along the shoreline at Dutch harbor to a depth of about 3 m. Each reef consists of two sub-areas 10 × 10 m each, one with cobble (10–20 cm in diameter, 25 cm above the seabed), and the other with boulders (20–40 cm in diameter, 50 cm above the seabed) (Castro, 1997). With funds from University of Rhode Island Sea Grant the reefs will be monitored over a period of 5 years to determine growth, immigration and emigration rates, competition between hatchery-reared and wild lobsters, and additional recruitment to the reefs by wild postlarvae. Some believe that this study may be the first step to the reestablishment of a Rhode Island hatchery (Nor'Easter, 1996). During the summer of 1997, tagging of lobsters and monitoring of the reefs were conducted with a total of 1,036 lobsters being caught at three sites: 1) artificial reefs, 2) off the reefs, and 3) Dutch Island. These lobsters ranged in size between 1.5 inch CL to 4 inch CL, with an average of 0.86 lobsters per m² (Castro, 1997). In 1998, Mount Desert Oceanarium Lobster Hatchery in Maine shipped 2,000 postlarvae to the University of Rhode Island Fisheries Center to join the 1,500 postlarvae that were reared at the university hatchery and the 300 provided by the New England Aquarium. Each lobster was to be micro-tagged for identification and placed on the artificial reefs for further studying (Tuttle, 1998).

Maine Propagation

As early as 1883, the legislature in Maine passed an act allowing the artificial propagation of lobsters. By 1887, R. T. Carver was granted the right to propagate lobsters in Carver's Pond, Vinal Haven, Maine. Unfortunately, this attempt was a failure, owing to the mud in the pond which killed all the larvae (Cobb, 1901). However, that did not

deter further attempts, and by 1904, a Federal hatchery was established at McKown's Point, Boothbay Harbor. Activities consisted of hatching detached eggs in McDonald hatching jars and releasing Stage I larvae, until about 1938 when a few Stage IV lobsters were reared experimentally and released (Taylor, 1950).

Meanwhile, during the mid-1930's a Maine delegation visited the Connecticut hatchery and, on the basis of their observations, established a state hatchery in Boothbay Harbor, just southeast of the Federal one (Dow, 1949; Carlson, 1955; Stickney, 1986). The Maine state hatchery ran in conjunction with the Federal hatchery in that eggs were hatched in the Federal facility and transferred to the state hatchery for rearing (Taylor, 1950; Taylor and Dow, 1958). By following the design used in Connecticut with some modifications (Anonymous, 1936), Maine reared and released in excess of 2.3 million Stage IV lobsters into their state waters over a 10-year period (Taylor, 1950; Taylor and Dow, 1958).

Massachusetts Propagation

In 1885, lobster culture was conducted on a very small scale by Richard Rathbun and Captain H. C. Chester working in Woods Hole and Gloucester, Mass. By 1886, several million eggs were hatched using the McDonald tidal box, the Chester jar, and the McDonald hatching jars (Bowers, 1900). Larval development was first observed at this time (Ryder, 1886b). During 1887–90, over 17 million eggs were collected and hatched with a 54% success rate. At the same time, the various methods were assessed, and the researchers determined that the McDonald jars outperformed the McDonald tidal box and the Chester jar. From 1890 to 1897, billions of eggs were hatched in the McDonald jars, with an 81–93% success rate (Bowers, 1900).

During 1898–99, emphasis shifted to rearing postlarvae instead of larvae. Several methods to do so were explored, including submerging the larvae in wooden cars and canvas bags (Sherwood, 1905). By 1903, researchers felt that environmental conditions in Gloucester

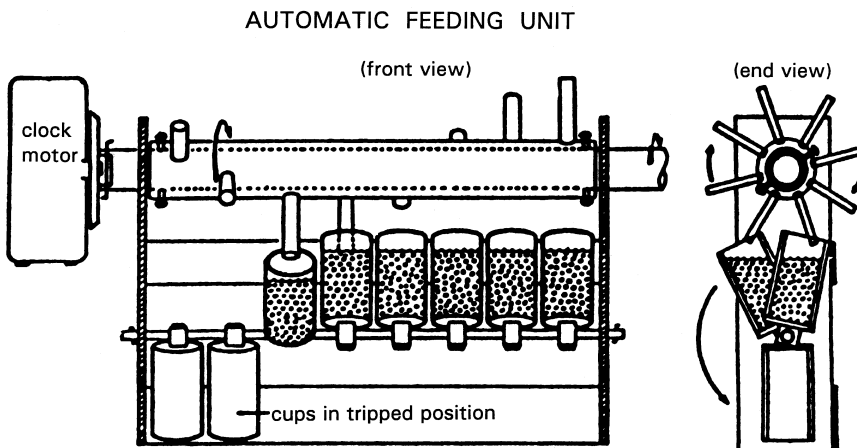


Figure 13.—Automatic feeding unit for the recirculating larval culture system. From Serfling et al. (1974b). Used with permission.

were not ideal for raising postlarvae, and suggestions were made to try other locations. Releasing of Stage I larvae continued, however, until 1917, when the Gloucester hatchery was closed (Sherwood, 1905; Carlson, 1955). Around 1937, the Gloucester hatchery reopened to hatch lobster eggs artificially and rear them to postlarvae, but in 1953, this hatchery once again ceased its activities.

In 1939 Massachusetts appropriated money to build a state lobster hatchery (Barnes, 1939) in Oak's Bluffs on Martha's Vineyard; however, the actual construction did not begin until after World War II (Anonymous, 1963). Unlike the hatcheries before it, this hatchery's purpose was both to rear and release Stage IV lobsters and to study the basic biology of the lobster (Anonymous, 1963; Kenslor, 1970; Syslo, 1986). Beginning operations in 1951, the Massachusetts State Lobster Hatchery and Research Station used rearing equipment similar to that developed by Capt. Banning at Connecticut's Noank hatchery (Carlson, 1954; Anonymous, 1964; Hughes and Matthiessen, 1967). From 1951 through 1963, 2 million Stage IV lobsters were reared and released, averaging 150,000 annually, with a survival rate of about 30% (Anonymous, 1963). Although annual releases increased to about 500,000, the hatchery's operations were terminated in 1997 so that its focus could shift to research projects only (Estrella⁶).

Canadian Propagation

In 1890, the first lobster hatchery opened in Newfoundland. Originally eggs were incubated in glass jars with aeration, but by 1893 this method of hatching eggs was replaced by the Nielsen incubator (Roché, 1898). By 1894, a total of 21 hatching stations were established with anticipation of the number reaching as many as 68. Each station hatched about a million eggs each year (Anonymous, 1895). In 1891, a hatchery, consisting of a building 45 × 35 ft, opened at Bay View, Nova Scotia (Corrivault and Tremblay, 1948). Eggs were collected from lobsters supplied by the canning factories and were incubated in McDonald hatching jars with aeration and agitation of the water (Roché, 1898). From 1903 to 1912, 15 additional hatcheries were established: 8 in Nova Scotia, 3 in New Brunswick, 2 on Prince Edward Island, and 2 in Quebec (Corrivault and Tremblay, 1948). The combined releases of larvae from these hatcheries was well over 2 billion (Herrick, 1911a), but in 1917 it was concluded that 1) the female lobster was a better incubator than artificial methods and 2) there was no evidence that hatchery efforts were enhancing the natural populations;

⁶ Estrella, B. 1998. Massachusetts Department of Marine Fisheries, 50A Portside Drive, Pocasset, MA 02559. Personal commun., Feb.

Table 4.—Approximate number of days required to pass through larval and postlarval stages at various temperatures.

Temp. (°C)	<i>H. americanus</i> ¹						<i>H. americanus</i> ²						<i>H. americanus</i> ³						<i>H. gammarus</i> ⁴						
	I	II	III	IV	I-IV	I-V	I	II	III	IV	I-IV	I-V	I	II	III	IV	I-IV	I-V	I	II	III	IV	I-IV	I-V	
8	20	26	42																						
10	14	15	25	49	54	103	13	18	25	54	56	110													
12	10	11	15	32	36	68	8	11	16	30	35	65													
14	7	8	11	25	26	51																			
15																									
16	5	6	9	22	20	42	6	7	9	23	22	45													
18	3	5	7	18	15	33	4	4	6	20	14	34													
20	2	4	6	14	12	(26)																			
22	2	4	5	11	11	(22)	3	3	4	14	10	24													

¹ Source: Templeman (1936).

² Source: Mackenzie (1988).

³ Source: Hughes and Matthiessen (1962).

⁴ Source: Havinga (1929), as cited in Scattergood (1949b).

thus all hatcheries were closed (Knight, 1918). Through the years several hatcheries were established in Canada for transplantation programs (Ghelardi and Shoop, 1968, 1972), to supply Stage IV postlarvae for studies on their ecology in coastal regions (Roberts, 1984), and with the purpose of exploring the biology of the lobster and aquaculture potential (Waddy, 1988).

The focus then shifted to broodstock management, where females and males were kept in captivity on a temperature-photoperiod cycle that mimicked that of their natural habitat (i.e. one where the water temperature rises above 12°C in the summer and drops to 5°C or lower in the winter). Normal female molting and spawning cycles were maintained and, by manipulating the photoperiod/temperature cycle, year-round production of larvae was achieved (Waddy and Aiken, 1991; Aiken and Waddy, 1995). Details of this broodstock facility located at the biological station at St. Andrews, N.B., can be found in Aiken and Waddy (1995). Despite the success of this program, the Department of Fisheries and Oceans closed this facility in the late 1980's.

Despite the successes in hatching eggs and rearing larvae beyond the postlarval stage, the United States hatcheries, as well as those in Quebec, France, and Norway, all were closed by 1955, with the exception of the one in Massachusetts. The reasons for their closure varied from being "biologically unsuitable" to "economically unjustifiable" (Knight, 1918; Taylor and Dow, 1958; Prudden, 1962; Wilder, 1965, 1971, 1972; Bardach et al., 1972). Taylor

(1950) reviewed lobster-rearing efforts in Maine, evaluating hatchery efficiency based on the percentage of survival from larvae (Stage I) to post-larvae (Stage IV). Carlson (1955) reviewed the efficiency of the Connecticut hatchery, considering biological, social, and economic factors. Both reports emphasized that hatcheries were not the proper vehicle for enhancing natural lobster stocks. However, during the years that the Wickford hatchery was in operation in Rhode Island, landings increased from <180 t to >726 t, which some researchers attributed to the releases of postlarvae (Carlson, 1954). Additional anecdotal evidence exists for other stocking programs (New York, Rhode Island, and Massachusetts) where sightings of abundant small lobsters have been assumed to be a product of hatchery reared stock (Anonymous, 1899; Mead, 1905; Bardach et al., 1972; Syslo, 1986).

In contrast, although the Massachusetts stock enhancement program has released millions of Stage IV lobsters into coastal waters, documented landings have not increased significantly. Such results suggest that few postlarval lobsters released ever reach commercial size. Barnes (1939) concluded that it is often difficult to determine just what benefits derive from lobster enhancement which supplements a naturally fluctuating supply of lobsters, particularly when protective measures are also in operation. Spanier (1994) suggested that lobsters reared in the absence of predators and other environmental cues and subsequently released into the wild might be at a higher risk of predation

because of their naiveté. In the absence of clear, easily recognizable tags for hatchery-reared lobsters, the impact they have on natural populations will continue to be difficult to assess. However, the best estimates of the economic impacts released lobsters have made upon the natural population at very low survival rates is presented in Table 4 (Syslo⁷).

Laboratory and Field Research Stemming From Hatchery Experimentation

During early hatchery operations, many aspects of lobster life history were examined. Ultimately these studies were justified as being important for improvement of culture methods and for providing life history data important for fisheries management. However, these studies also provided the basis for many current experiments. While it is impossible in such a review to describe every experiment on homarid lobsters, brief outlines of the most important work are presented.

Embryology

Several early studies focused on *H. americanus* and *H. gammarus* embryology. Herrick (1891a, b; 1895) described the developmental rates of *H. americanus* embryos at temperatures of 20°–22°C and their prelarval stages. From these data, he was able to calculate the approximate date of extrusion.

⁷ Syslo, M. 1989–92. Massachusetts State Lobster Hatchery and Research Station, P.O. Box 9, Vineyard Haven, MA 02568. Personal commun., var. dates.

Bumpus (1891) described structures and illustrated the various developmental stages. Although these stages of development were not documented with varying temperatures, Bumpus' data describe a "primary egg-membrane" which proved useful in later studies on osmoregulation by embryos (Charmantier and Aiken, 1987). Similar descriptions were provided for *H. gammarus* by Fullarton (1896).

Templeman (1940a) presented information on the time required for *H. americanus* to reach the 16-cell stage up to the formation of eye pigment at various temperatures. Perkins (1972) then determined the rates of development, the time required to complete the embryonic period, and subsequent hatching time at various temperatures for *H. americanus*. Hepper and Gough (1978) examined the development of embryos of *H. gammarus* during different times of the year. However, they did not manipulate temperatures during rearing conditions. Nonetheless, their information has been useful for calculating time of hatching (Burton, 1992). Richards and Wickins (1979) used Perkins' (1972) formula to provide similar information for *H. gammarus*, but used only one temperature regime of 13°–15°C. The data of Perkins (1972) and Richards and Wickins (1979) have been used in several lobster hatcheries to schedule year-round larval production (e.g. Schuur et al., 1976; Castell, 1977; Waddy and Aiken, 1984a, b; Beard et al., 1985).

More recently, Helluy and Beltz (1991) examined the embryonic period and subsequent hatching time at various temperatures for *H. americanus* from the formation of the naupliar stage until the emergence of the first larval stage. They provided a percent-staging system based upon Perkins' (1972) eye index, with a quantitative characterization of 10 embryonic stages. Anatomical and morphological observations of earlier researchers (e.g. Bumpus, 1891; Herrick, 1895) were then related to this staging system. In support of both Bumpus' and Herrick's claims of embryonic molts, Helluy and Beltz (1991) presented evidence for two molts prior to the first larval stage which were

associated with the beginning and end of the embryonic metanaupliar stage. The characterization of the metanaupliar molt cycle and the percent-staging system should prove useful for future investigations of neural, physiological, and ecological aspects of *Homarus* embryonic life, as well as for evolutionary comparisons with other decapod species (Helluy and Beltz, 1991). Similarly, Charmantier and Mounet-Guil-laume (1992) determined the rate of development for embryos of *H. gammarus* for various temperatures by measuring the size of their eyes and calculating the eye index according to Perkins (1972). They discovered that the slopes of equations for *H. gammarus* are nearly identical to those for *H. americanus*, indicating similar effects of temperature on the developmental rate of both species.

In nature, lobster ova develop internally for about 1 year (Aiken and Waddy, 1980; Waddy and Aiken, 1991); after extrusion, development can vary from 9 to 12 months depending on temperature (Bumpus, 1891; Herrick, 1911a; Templeman, 1940a; Aiken and Waddy, 1980, 1986; Waddy and Aiken, 1991). This also holds true for *H. gammarus* (Fullarton, 1896; Branford, 1978; Hepper and Gough, 1978; Burton, 1992). The duration of the hatching period is also determined by temperature and can vary from a few days to several weeks (Herrick, 1911a; Hughes and Matthiessen, 1962; Goggins and Fortier, 1964; Ennis, 1975a). Once hatching begins, the larva emerges from the egg as a "pre-larva" and usually molts into the first larval stage before being released by the female (Herrick, 1911a; Davis, 1964; Ennis, 1975a; Charmantier and Aiken, 1987; Charmantier et al., 1991). The time required for Stage I larvae to molt to Stage IV can vary considerably, from 11 to 42 days. Water temperatures of 22°C result in 11 days of development, while 8°C results in 42 days. Hughes and Matthiessen (1962) reported similar periods of 9 days at 22°C and 32 days at 14°C to reach Stage IV. The duration of the postlarval stage also varies with temperature from 11 to 49 days at temperatures of 22°C and 10°C, respectively (Templeman, 1936;

Aiken, 1980). More recently, Mackenzie (1988) examined the temperature dependence of stage duration, survival, and body size for larval and postlarval stages. Time to reach Stage IV varied from 10 to 56 days at 21°–22°C and 10°C, respectively. Stage IV postlarvae required 14 to 54 days to reach Stage V at 22°C and 10°C, respectively. Total cumulative survival, defined as the number of larvae reaching Stage V divided by initial sample size of Stage I larvae, was 4, 56, 64, 68, and 47% at 10°, 12°, 15°, 18°, and 22°C, respectively. Dry weight of larvae increased nearly tenfold during development from Stage I to Stage V, and Stage V lobsters cultured at 15°C and 18°C were larger than those cultured at other temperatures (Mackenzie, 1988). In spite of the different methodologies used by the above researchers, stage durations were within one standard deviation (Mackenzie, 1988). *Homarus gammarus* experiences similar growth variations at corresponding temperatures (Sund, 1914; Havinga, 1929, cited in Scat-tergood, 1949b; Richard and Wickins, 1979; Beard et al., 1985; Burton, 1992). Table 5 summarizes the development (in days) for larvae to reach Stage IV and V at various temperature regimes.

Description of Morphological Changes

Morphological changes during larval development and metamorphosis have also been extensively studied. The first descriptions were made by Smith (1872) using larvae sampled from Vineyard Sound, Mass. and adjacent waters. Smith observed three larval stages and a fourth stage which resembled the adult. Fourteen years later, Ryder (1886b) confirmed Smith's observations while rearing larval lobsters in confinement at the Woods Hole, Mass., hatchery. These studies were followed by the comprehensive and beautifully illustrated work of Herrick (1895, 1911a). His line drawings of larvae and postlarvae have been reproduced and modified many times (by Chaikelis, 1953; Taylor, 1975; Cobb, 1976; Phillips and Sastry, 1980; Aiken and Waddy, 1986, 1989; Anonymous, 1988; Charmantier et al., 1991; White, 1991). Hadley (1906a)

Table 5.—Economic value of hatchery-reared lobsters seeded into local waters, based on various survival rates after release. Survival rates are based on the release of 500,000 Stage IV postlarval lobsters.

Survival rates	Pounds harvested		1986 Ex-vessel worth	=	Value to lobsterman	×	Fisheries economic multiplier ¹	=	Total economic value	×	Fisheries economic multiplier ²	=	Total economic value
5%	25,000	×	3.14/lb	=	\$78,500	×	2.8	=	\$219,800	×	4.5	=	\$353,250
10%	50,000	×	3.14/lb	=	\$157,000	×	2.8	=	\$439,600	×	4.5	=	\$706,500
15%	75,000	×	3.14/lb	=	\$235,500	×	2.8	=	\$659,400	×	4.5	=	\$1,059,750
20%	100,000	×	3.14/lb	=	\$314,000	×	2.8	=	\$879,200	×	4.5	=	\$1,413,000
25%	125,000	×	3.14/lb	=	\$392,500	×	2.8	=	\$1,099,000	×	4.5	=	\$1,766,250

¹ Source: Blake (1991) for 2.8 economic multiplier.

² Source: Mike Syslo, Massachusetts State Lobster Hatchery and Research Station, P.O. Box 9, Vineyard Haven, Mass. 02568. Personal commun. 30 Mar. 1990.

also produced beautiful line drawings, but these have proven to be less popular than those of Herrick and have only been used occasionally (Fig. 14 and by Beasley, 1904; Mead, 1910; Nigrelli, 1936; Barnes, 1939; Cook, 1972; Factor, 1995). Herrick also provided the criteria for distinguishing the individual larval stages which are still used by researchers today (Harding et al., 1982; Matthiessen and Scherer, 1983; Gunn, 1987; Blake, 1988, 1991, 1993; NUSCO, 1989, 1990).

Couch (1843, reported in Williamson, 1905) was the first to describe the prelarval stage for the European lobster *H. gammarus*. Sars (1875) subsequently described and illustrated the three larval stages. Williamson (1905) also described and illustrated the larval and postlarval stages, and Chadwick (1905) described the pre-larval, larval, and postlarval stages. More recently, Nichols and Lawton (1978) diagrammed Stage I to Stage IV lobsters; these diagrams (Fig. 15) are now

used to distinguish larval stages during culturing experiments (Richards and Wickins, 1979; Beard et al., 1985; Burton, 1992).

Larval Migrations

Attempts to understand the vertical and horizontal migrations of the larvae resulted in a flurry of research that began over 100 years ago. Smith (1872, 1873) was apparently the first to sample for larvae in Vineyard Sound and the adjacent waters. Using a hand or towing net, he observed that the planktonic stages seemed to inhabit only the surface waters. Smith's observations were confirmed by subsequent researchers using simple plankton sampling methods (Mead and Williams, 1903; Herrick, 1911a; Templeman, 1937; Squires, 1970; Lund and Stewart, 1970; Scarrott, 1973a; Harding et al. 1979, 1982; Hudon et al. 1986). With more sophisticated sampling techniques, however, Matthiessen and Scherer (1983) found the highest concentrations of larvae at a depth of 3 m. More recently, Harding et al. (1987) found that larval lobsters were capable of vertical migrations to depths of 30 m in oceanic waters. The phototactic responses of the larvae can influence such vertical migrations. Herrick, experimenting in 1894, was apparently the first to discover that the behavior of larval lobsters is strongly influenced by light (Herrick, 1911a). However, it was not until the extensive experiments of Hadley (1905, 1908) with *H. americanus* and of Böhn (1905) with *H. gammaurus*, that the effects of light intensities on larval behavior were understood. Hadley (1905, 1908) found that phototactic responses of larvae changed both within and between each stage. Böhn (1905) observed similar trends in *H.*

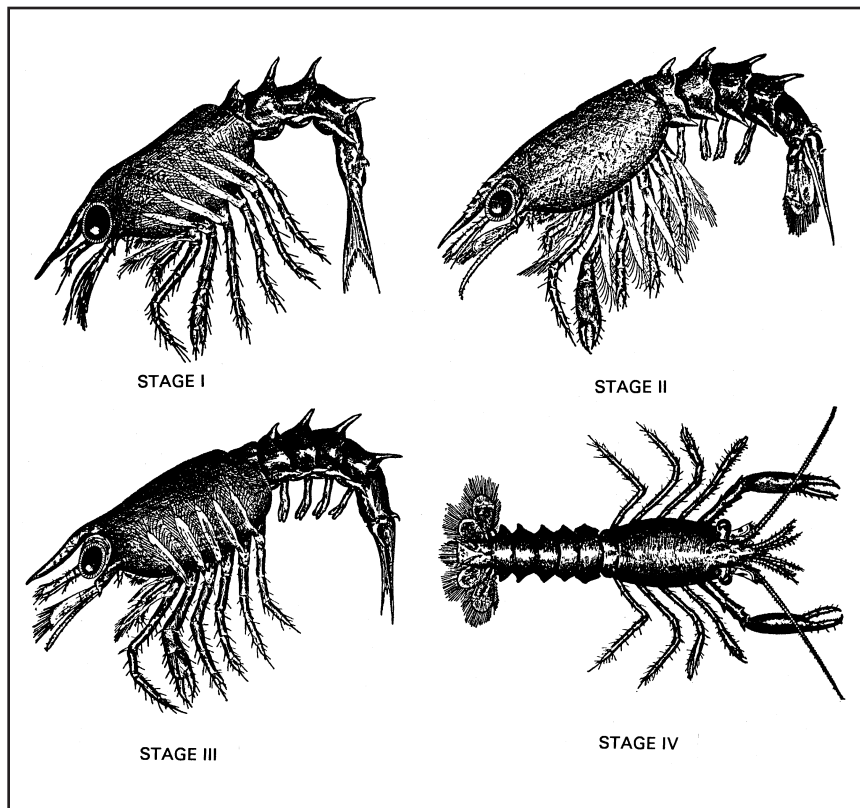


Figure 14.—Larval and postlarval American lobsters (*Homarus americanus*) showing Stage I, II, and III larvae and a Stage IV postlarva. (From Hadley, 1906a).

gammarus (reported by Herrick, 1911a). Within the first few hours following hatching, Stage I larvae were attracted to a light source of high intensity, but this response was reversed by the second day. However, Stage I larvae were still attracted to reduced light levels (Hadley, 1908). Harding et al. (1987) concluded that Hadley's results anticipated not only the vertical migration due to light intensity, but also explained why most Stage I larvae remained at the surface throughout the day as found by Lund and Stewart (1970), Scarratt (1973a), Harding et al. (1987), and Strube (1989).

Stage II and III larvae are also positively phototactic several hours before molting; postmolt they become negatively phototactic (Hadley, 1908). This result is consistent with the reduced numbers of Stage II and III larvae found in the surface samples of Lund and Stewart (1970), Scarratt (1973a), Harding et al. (1987), and Strube (1989) and suggests that Stage II and III larvae migrate downward to avoid high light intensities.

While phototaxis plays an important part in regulating vertical migrations and may allow the larvae to maintain or control their position, traditional thought held that larvae were merely passive drifters transported by surface currents (Herrick, 1894; Mather, 1894; Templeman, 1940b; Scarratt, 1964; Stasko, 1978; Matthiessen and Scherer, 1983; Hudon et al., 1986). However, detection of turbulence induced by wind or surf close to the shore may trigger vertical movements (Squires, 1965, 1970; Squires et al., 1971; Caddy, 1979), enabling the larvae to utilize subsurface currents moving in different directions as a mechanism to avoid long distance displacement by surface currents (Ennis, 1986a).

Planktonic stages also react to pressure, suggesting that modulation of depth is possible (Ennis, 1975b). Thus, researchers hypothesized that movements of larvae were progressively inshore due both to predominant inshore currents during the same months that larvae are present, and the ability of the larvae to regulate their depth (Stasko, 1978; Harding et al., 1982, 1987; Harding and Trites, 1988, 1989).

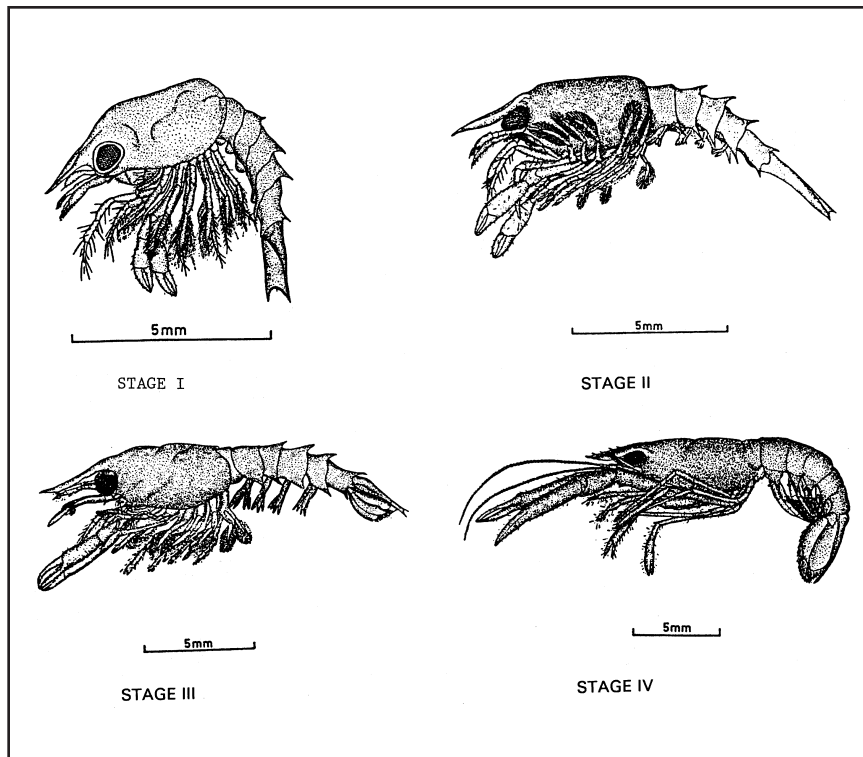


Figure 15.—Larval and postlarval European lobsters (*Homarus gammarus*) showing Stage I, II, and III larvae and a Stage IV postlarva. (From Nichols and Lawton, 1978). Used with permission.

Other factors associated with the survival, growth, and development of lobster larvae also have received much attention. These include, but are not limited to, light, food, salinity, disease, mutilation, social environment, and water quality (e.g. Templeman, 1936; Cobb, 1968, 1970; Ford et al., 1976; Sastry and Pechenik, 1977; Aiken, 1980; Phillips and Sastry, 1980; Charmantier et al., 1984; Aiken and Waddy, 1986; Jackson and Castell, 1989; Burton, 1992; Corey²).

Metamorphosis and Settlement

Metamorphosis occurs at the fourth molt (from Stage III to IV) and results in a postlarvae which is different, not only in form, but also in behavior, from the previous stages (Hadley, 1906b). The postlarva is morphologically similar to the adult, but lacks the asymmetrical claws and has a longer abdomen. Hadley (1908) noted that Stage IV postlarvae were positively phototactic at the beginning of the stage and actively sought greater intensities of light, which

explained the large numbers of Stage IV postlarvae caught in surface samples (Stasko, 1977; Greenstein et al., 1983; Hudon et al., 1986; Blake, 1988). Between the early and late parts of Stage IV, the phototactic response changes dramatically and permanently, becoming negative (Hadley, 1908; Scarratt, 1973a; Botero and Atema, 1982). This change in phototaxis explains the lobster's observed preference for dark shelters beginning with the postlarval stage and continuing into the juvenile stages (Cobb, 1971; Botero and Atema, 1982; Johns and Mann, 1987; Boudreau et al., 1990). It may also partially explain the adoption of a benthic lifestyle midway through or near the end of the stage (Herrick, 1895, 1911a; Botero and Atema, 1982; Charmantier et al., 1984, 1991; Cobb et al., 1989a; Corey²), when postlarvae settle into the benthic environment (Scarratt, 1973a; Cobb et al., 1989a).

Despite the early observation that postlarval lobsters were capable of

swimming with greater speed and precision than any of the preceding stages (Smith, 1873; Williamson, 1905; Herrick, 1911a), it was not until the studies of Ennis (1986b), Cobb et al. (1989b), and Rooney and Cobb (1991) that the significance of strong and well-directed swimming for inshore recruitment was understood. Katz et al. (1994) point out that currents and wind-induced transport alone are insufficient in and of themselves for offshore recruitment of larvae to coastal populations, although when combined with strong directional swimming of the postlarvae, they may allow long-distance recruitment from offshore to inshore sites.

Other studies reveal that nearshore environments are not necessarily where postlarval lobsters settle. Briggs (1975, 1985, 1987, 1989, 1990, and 1991) found juvenile lobsters as small as 7, 16, 17, 22, 24, and 26 cm CL in considerable numbers from traps in the deeper waters off Long Island Sound, New York. Blake (1991) also found juvenile lobsters the size of >17 mm CL in samples from the Connecticut side of Long Island Sound. Therefore, postlarval and juvenile lobster sampling should not be limited to nearshore environments, but should also be conducted in deeper waters, so that we can understand what role deeper water juvenile populations may play in the recruitment to the fishery.

It should be noted that thermoclines ($\geq 5^{\circ}\text{C}$ difference) may provide a barrier to most settling postlarvae. It is not until they are much further along in Stage IV (15 days postmolt), that they will pass through such thermoclines (Corey²). Recently, Boudreau et al. (1992) and Hofe (1994) have more rigorously tested the effects of thermoclines on settling postlarvae and have determined that both larvae and postlarvae remain above the thermocline if it is of at least a 5° – 6°C difference, but postlarvae will pass through a thermocline as the temperature difference between it and the upper waters decreases (Boudreau et al., 1991, 1992). This may be one of the reasons that the greatest densities of new benthic recruits are found in shallow waters. With increasing depth, densities of new recruits tend

to decline to those typically found in poorer habitat types (i.e. eelgrass, mud, etc.) (Wilson and Steneck⁸)

The variability in timing of settlement observed by Cobb et al. (1989a) confirms earlier observations of Herrick (1911a) that such timing is not fixed. Furthermore, both Cobb (1968) and Botero (1980) observed that Stage IV lobsters can delay molting to Stage V if not presented with a suitable substrate. These laboratory observations were confirmed by field observations of postlarval lobsters swimming over and repeatedly diving to examine substrates (Cobb et al., 1983). Havinga (1929, cited in Scattergood, 1949b) also noted that the swimming abilities of *H. gammarus* postlarvae could be very useful during their search for a suitable benthic substrate. Experiments by Boudreau et al. (1990) supports the hypothesis that settling postlarvae can make an active benthic choice of microhabitat and will delay settlement if not provided with suitable conditions. Delays in settlement are supported by higher proportions of late molt stage postlarvae found in plankton samples (Cobb et al., 1989a; Inze and Wahle, 1991). Cobb et al. (1989a) and Bertran et al. (1985) provide some theories as to how postlarvae may prepare for settlement into benthic environments for *H. americanus* and *H. gammarus*, respectively. The postlarvae obtain information about potential settlement sites by diving down to the substrate, touching down directly on its surface, and lifting-off, if it is deemed unsuitable. By reentering the water column, the lobster can use the currents to sample a wider range of bottom types (Cobb et al., 1989a).

Burrowing Behavior

Burrowing behavior has also been closely examined. Mead (1901) determined that burrowing behavior first appears in Stage IV and becomes more pronounced in the succeeding stages of *H. americanus*. Cobb (1971) confirmed those observations. *Homarus gammaurus* also begins burrowing activity in

the fourth stage (Berrill, 1974). In contrast, the postlarval stage of *N. norvegicus* is assumed to first enter the burrow of an adult before forming its own shelter (Howard, 1989). Herrick (1911a) remarked on the burrowing behavior, "...when a bottom life is adopted, the instincts of burrowing, hiding, wariness, pugnacity and preying become strongly accentuated, that at this stage it betrays fear and caution, digs burrows and hides." Herrick (1911a) concluded, "...burrowing is a kind of behavior in which the lobster frequently indulges from the fourth stage [late Stage IV] onward throughout life. In a word, their behavior is no longer variable, but is in measure 'stereotyped'."

Cobb (1971) concluded that the behavior involved in burrow excavation is not "stereotyped," but may be modified to suit the type of burrow being constructed and the type of substrate. However, Botero and Atema (1982) confirmed Herrick's conclusion and described the stereotypical burrowing behavior for *H. americanus*. Howard and Bennett (1979) have described behavior remarkably similar for *H. gammarus*, as have Dybern and Höisaeter (1965) and Rice and Chapman (1971) for *N. norvegicus*.

Mead and Williams (1903) noted a marked preference for certain nooks, burrows, and other places of concealment. Cobb (1971), Pottle and Elner (1982), Lawton (1987), Boudreau et al. (1990), Wahle (1992b), Dybern (1973), Howard (1980), and Howard and Bennett (1979) have confirmed the preference that *H. americanus* and *H. gammarus* exhibit for certain sizes of shelters. Others have described the burrowing behavior in various substrates, such as mud, silt/clay, rocks, and eelgrass (Mackay, 1926, 1929; Ennis, 1968; Cobb, 1971; Berrill and Stewart, 1973; Botero and Atema, 1982; Pottle and Elner, 1982; Barshaw and Bryant-Rich, 1988). Experimental introductions of *H. americanus* along the Pacific coast of Japan (Kittaka et al., 1983) showed that 1-year-old lobsters used burrowing methods (under cement blocks) similar to those described by Cobb (1971), Dybern (1973), and Cooper and Uzmann (1980).

⁸ Wilson, C., and R. Steneck. 1998. Personal commun. 14 April and 14 June. Univ. Maine, Darling Mar. Lab., Walpole, ME 04573.

Substrate Selection

Interest in the appropriate substrates for settling postlarvae has also spurred much research. The stereotypical and efficient burrowing behavior exhibited not only by *H. americanus*, but also *H. gammarus* and *N. norvegicus*, suggested that lobsters were particularly suited to soft substrates (Berrill and Stewart, 1973; Berrill, 1974; Botero, 1980). As early as 1895, Herrick considered that eelgrass may be a potential habitat for lobsters. MacKay (1920, 1929) confirmed this when he found small lobsters in mixtures of sand, mud, and eelgrass. Barshaw and Bryant-Rich (1988) conducted a long-term study on the behavior and survival of early juvenile lobsters in three naturalistic substrates: eelgrass, mud, and rocks. They found that postlarval lobsters took less time to burrow into eelgrass and had higher rates of survival compared to postlarval lobsters in mud and rocks. Furthermore, lobsters in eelgrass were larger, despite the higher densities of animals. However, predation experiments using eelgrass (Barshaw and Lavalli, 1988) suggest that eelgrass is a suboptimal environment for predator avoidance but does sustain intermediate levels of survival when compared to that of sand environments. Heck et al. (1989) conducted trawl sampling from eelgrass areas on Cape Cod, Mass., and found only low densities of lobsters. Their study concluded that eelgrass meadows were not significant nursery areas; however, their sampling method differed greatly from the more successful air-lift sampling technique of Able et al. (1988) and Wahle and Steneck (1991). Peat reefs are also intermediate in their protective quality (Barshaw et al., 1994); nonetheless, relatively high densities of juvenile lobsters have been found in peat. Morrissey (1966) discovered postlarval and juvenile lobsters in salt marsh areas and around sod clumps in the Nauset Harbortown Cove area of Orleans, Mass. Approximately 135 m of shoreline were sampled in each instance. On the three sampling dates, lobsters captured ranged in size from 7 to 83 mm CL. Morrissey (1966) also observed a vertical gradation by size, with smaller

individuals (< 40 mm CL) being located in the upper portion of large sod clumps and in smaller clumps of shallow slope areas. Larger lobsters (> 40 mm CL) occupied large rocks or were found under boulders in deeper waters. More recently, Able et al. (1988) found postlarval lobsters in densities of 2.1 individuals/m², ranging in size from 6 to 72 mm CL (mean of 26.7 mm CL), in peat beds near salt marshes of Cape Cod.

While densities vary, substrates other than peat or eelgrass provide shelter for recently settled lobsters. A. M. Olsen (Senior Research Officer, DFO, CSIRO, Australia) captured 32 lobsters (of about 17–69 mm CL) by hand in 35 minutes off Richibucto, New Brunswick, during a visit (reported in Wilder, 1959). He observed that lobsters were not only numerous on rocky bottoms, but also on smooth, firm sandy/silt. Some were partially or completely hidden under large flat stones. Many, however, were seen moving freely about (reported by Wilder, 1959). National Marine Fisheries Service (NMFS) divers examined mud substrates in central Maine harbors during July through September 1975 and found densities of Stage IV to XI lobsters of 1–20/m². Nearly all individuals were retrieved from tiny burrows excavated next to solid objects (e.g. lumber, discarded shoes, bottles) that are the type of refuse commonly discarded into waters of an intensively utilized harbor. Very few lobsters were found in mud substrates which lacked overlying rocks, gravel, or other solid objects (Cooper and Uzmann, 1977).

Ennis (1968) found that Stage VI juveniles were capable of building depressions in sand and mud after a period of time spent wandering over these substrates, but ultimately preferred rocks and would take shelter immediately upon contact with them or would shift to sheltering under rocks if they were subsequently introduced onto the mud and sand substrates. Hudon and Lamarche (1989) found no postlarval lobsters of 5–31 mm (CL) on sand or on sand and eelgrass, but reported densities of 1.4/m² in bare rocks and 1.3/m² in rocks with algae. Wahle and Steneck (1991) observed 5–40 mm CL lobsters at maximum densities of 16/m²

in quadrats with 100% cobble cover. These results are similar to laboratory experiments of Van Olst et al. (1976a), where they observed densities of 6–30 lobsters/m² ranging in size from 14 to 18 mm CL, depending on the substrate. Conversely, densities up to 62/m² were observed on rocky bottoms in semienclosed basin experiments carried out with *H. gammarus* (Bertran, 1984). While Wahle and Steneck (1991) report that cobble may appear to be a preferred habitat for postlarval lobsters, others (MacKay, 1920, 1929; Morrissey, 1966; Cooper and Uzmann, 1977; Able et al., 1988) have shown that postlarval lobsters use various substrates; thus, eelgrass, peatbeds, or mud can and will be used as alternate habitat where cobble may be lacking.

Surprisingly, lobsters have also been found in the intertidal zone. Krouse (1983), during a tag-recapture program conducted from 1977 through 1982, caught lobsters ranging in sizes from <10 to ~80 mm CL, by hand in the intertidal zone of Maine's Sheepscot River. Substrate there ranged from fine to coarse sand intermingled with broken shell with scattered rocks of various sizes (from barely moveable to many of grapefruit size). This substrate is found adjacent to large bedrock ledges covered with seaweed (Krouse⁹). Similarly, Cowan¹⁰ and Cowan (1999) found small-to-moderate densities (0–8.6 individuals/m²) of intertidal lobsters ranging in size from 3 to 42 mm CL, at Lowell's Cove, Orr's Island, Maine, and in selected rocky areas throughout the New England states (N.H., Mass., R.I., Conn.). These lobsters are typically found under scattered rocks on the beach surface.

Despite finding lobsters in vegetated, rock, and intertidal habitats, Wahle and Steneck (1991) suggest that soft substrates of mud or those with vegetation, such as eelgrass and peat, are rarely used by settling postlarvae. Support for

⁹ Krouse, J. S. 1992. Department of Marine Resources, Mar. Resour. Lab., McKown Point, West Boothbay Harbor, ME 04575. Personal commun. 6 July.

¹⁰ Cowan, D. F. 1992–96. Department of Biology, Bates College, Lewiston, ME 04240, and The Lobster Conservancy, P.O. Box 193, Orr's Island, ME 04066. Personal commun., var. dates.

their hypothesis comes from their extensive sampling efforts in cobble environments along the coasts of Maine, New Hampshire, and northern Massachusetts (Gulf of Maine). Densities of small lobsters (<40 mm CL) found by them are some of the highest reported; however, sampling efficiency of the air-lift suction process they use has not been established for the varying environments (mud, cobble, eelgrass). Wahle and Steneck (1991) sampled to a depth of 15 cm, while Cooper and Uzmann (1977, 1980) observed postlarval and juvenile lobster burrows as deep as 70 cm.

Able et al. (1988) observed that larger lobsters (>40 mm CL) build burrows to a 99 cm depth. Howard (1989) reported that *N. norvegicus* constructed burrows 20–30 cm below the mud surface. Wahle and Steneck (1991) relied on the laboratory studies of Berrill and Stewart (1973) and on their own observations for determining their sampling depth. However, laboratory experiments on burrowing behavior in 8–12 cm substrates found burrows to be 9 cm deep (Berrill and Stewart, 1973). Lobsters may have been restricted from digging further by the bottom of the tank. With substrates 8 cm deep, lobsters burrowed to a depth of 2.6 cm (Botero and Atema, 1982). In contrast, Howard and Bennett (1979), experimenting with *H. gamma-rus*, used substrates 40 cm deep and found that postlarval lobsters regularly burrowed to a depth of 15 cm, with a single instance of an 8 mm CL lobster burrowing to a depth of 25 cm.

Considering the stereotypical burrowing behavior and ecological similarities of these three species, the actual depth to which the postlarvae can burrow is quite variable. The differences in depth and sampling techniques used by Hudon (1987) and Wahle and Steneck (1991) could explain the limited numbers of lobsters found in mud and eelgrass, respectively. Therefore, until sampling techniques are tested for their efficiency in each substrate type, extrapolation of laboratory results for guidance in sampling protocols should be used with caution.

Environments which provide the best protection from predators include cobble,

or rocks upon rocks (Lavalli and Barshaw, 1986; Johns and Mann, 1987; Barshaw and Lavalli, 1988; Wahle, 1991b; Wahle and Steneck, 1991), as well as small stones embedded in sand and boulders with macroalgae (Hudon, 1987; Hudon and Lamarche, 1989). These substrates either require minimal burrowing activities or allow lobsters to probe spaces between rocks and immediately occupy appropriately sized spaces (Wilder, 1957; Wahle, 1992b). However, Roach (1983) experimenting with caged environments in the field found that survival and growth was higher in mud substrates, followed by vegetation and then rock. Unfortunately, the lack of consistent trends (such as reduced predation and high survival and growth) from these studies has made an accurate portrayal of benthic recruitment for postlarval lobsters difficult.

Feeding Activity

Research has also targeted the feeding activities of larval and postlarval lobsters. Williams (1907) examined the stomach contents of 100 larvae and postlarvae taken from the hatching bags at Wickford, R.I., and noted that they consisted primarily of copepods and diatoms. Herrick (1911a) found that the stomachs of larval lobsters examined from laboratory aquaria and Vineyard Sound, Mass., contained diatoms, crustaceans, bacteria, algae, and amorphous matter. Templeman (1933) reported that larvae reared on a full ration of copepods exhibited higher survival rates than those fed half, quarter, or one-eighth rations of copepods. Harding et al. (1983) discovered that Stage I and II larvae, taken from St. George's Bay, Nova Scotia, consumed cladoceran podons and copepods, while Stage III and IV lobsters consumed copepods, gastropod larvae, and crab larvae. Hargrave et al. (1985) found that the larval lobster's natural diet is composed of organisms in the 210–610 μm range, and that prey size increases as the larvae grow, with late stage larvae preferentially consuming more crab zoea and megalops larvae. Gunn (1987) noted that larvae from Long Island Sound consumed mostly crab larvae and copepods, with occasional cladocerans, insects, and diatoms.

She also confirmed the conclusions of Hargrave et al. (1985) that as larvae progressed through each stage, their prey size increased. Similarly, Juinio and Cobb (1992) found that copepods and crab larvae were the most common items in planktonic, postlarval lobster stomachs, with fish eggs and insects also frequently found. Based on gut fullness and condition of gut contents, Juinio and Cobb (1992) concluded that postlarvae fed throughout the day intermittently and at all stages of the molt cycle. Furthermore, by comparing growth rates of wild and laboratory-reared lobsters via RNA:DNA ratios, Juinio and Cobb (1994) confirmed Wilder's (1953) earlier observation that laboratory-reared larvae grow more slowly than their wild counterparts.

However, there is a caveat to these results in that growth rates of laboratory-reared larvae will be highly dependent on the type of brine shrimp used during culture, and different brands of brine shrimp can vary tremendously in lipid content and overall quality (Fujita et al., 1980; Eagles et al., 1984). Furthermore, the water supply can also provide additional food items (see below), if it is not filtered. Thus, the culture techniques of Juinio and Cobb (1994) must be considered when comparing wild and laboratory-reared larvae.

Survival studies indicate that settled postlarval and small juvenile lobsters are also capable of surviving and growing on planktonic diets. Emmel (1908) was the first to show this ability when conducting feeding experiments with artificial diets (e.g. beef, clam, lobster muscle, shredded fish, and beef liver) for hatchery operations. Postlarval lobsters on artificial diets were compared to those fed nothing, getting only that which entered with the water supply. Instead of starving, Stage IV postlarvae were able to molt into Stage V, albeit at a slower rate than those on a feeding regime. Barshaw (1989) also showed that postlarval lobsters could survive well on planktonic diets, but exhibited molt delays after Stage V when compared to those fed artificial diets. However, her data were complicated by unequal amounts of food fed for the two groups of lobsters.

Lavalli (1991) repeated and extended Barshaw's experiments, finding that postlarvae were capable of surviving throughout their first season on diets of plankton in the size range of 95–1,000 μm ; however, these lobsters were incapable of surviving on diets consisting mostly of diatoms. Lavalli (1992) determined with videoanalysis that juvenile lobsters were capable of suspension feeding. More recent studies have shown that adult European lobsters can also benefit from suspension feeding on plankton (Loo et al., 1993). Therefore, it is not surprising that Japanese researchers have successfully reared homarid larvae by utilizing a mixture of phyto- and zooplankton cultures previously developed for culture of penaeid shrimp (Kittaka, 1990). Development of the larvae to Stage IV at 20°C in outdoor tanks takes about 2 weeks. At a stocking density of 10 individuals/liter, the survival rate was 50% (Kittaka, 1990).

Tagging and Movement

Examination of the movements of adult lobsters and the development of tagging methods also began in hatchery settings. Bumpus (1901a) tagged 497 female lobsters (with eggs recently removed) with copper tags attached to their rostrums. These females were liberated at various points along the coast near Woods Hole, Mass. Within 4–89 days, 76 of the females were recaptured, some from as far as 25.6 km away. Migratory females moved in a southwesterly direction, while nonmigratory lobsters remained in the local waters for several weeks. Homing behavior was observed as several lobsters returned to the place where they were captured prior to tagging and release. Mead and Williams (1903) tagged 112 adult lobsters in 1902, using the same technique as Bumpus. They liberated these lobsters at Wickford, R.I., and within 1–11 days, 16 were recaptured. An additional 385 adults were tagged and liberated in 1903, and within 1–59 days, 62 were recaptured. Southerly movements of up to 17.6 km were recorded (Barnes, 1906b).

Although these tagging experiments were exploratory and inconclusive, they

did provide several theories on the direction and extent of lobster movements. Thereafter, many tagging studies focused on tag retention. Templeman (1935, 1940c) clipped metal tags to the telson of sublegal and legal-sized lobsters. Plastic or metal discs attached by wire to the second segment of the cheliped were used by Wilder (1947, 1953) in Canada, Thomas (1955) in Scotland, and Simpson (1961) in Wales. Wilder (1954) used a metal strip bent to form a hook at one end. This hook was inserted into the posterior margin of the carapace and kept in position along the mid-line by an elastic band attached to the other end and passed over the rostrum. These tags were quite successful, but were not retained through successive molts. Another method developed by Appelløf (1909b) and employed by Dannevig (1936), Wilder (1953, 1963), and Wilder and Murray (1956) was to punch or drill holes in the tail fan. This method was not only successful but lasted through several molts until the flesh grew back and filled the hole, but it was not completely reliable and depended on the grow rate of the lobster; Simpson (1963) provides a review. While these external tags provided some information to lobster managers, they were incapable of providing long-term movement information, as well as information on growth rates.

In 1963, John Hughes, Director of the Massachusetts State Lobster Hatchery and Research Station, experimented with several prototype tags. The "spaghetti-dart" was made of various colored vinyl plastic tubing (about 2 mm in diameter) attached to a small flexible double-barbed nylon dart. Only the dart and a small portion of the tubing was inserted into the lobster, with about 62.5 mm remaining exposed (Anonymous, 1965). The multi-barbed tag with a dart-like spear was about 25 mm by 6.4 mm with a 1.6 mm diameter, 75 mm long plastic "spaghetti" tube attached. Then a larger tag was tried (30 mm long by 8 mm wide) with a multibarbed dart having an eight-pronged barb (Anonymous, 1965).

Several tagging studies used these tags in various locations along the bodies of sublegal and legal-sized lob-

sters (e.g. telson, dorsal side of the third segment of the large claw, between the carapace and abdomen in the body cavity, and in the elbow of the large claw (Anonymous, 1965)). Results indicated that these tags could be retained through only one molt (Anonymous, 1966), but the "sphyrion" tag, a modified spaghetti-dart tag, remained through molting. This tag consisted of an anchor made of stainless steel wire with a double strand of polyethylene monofilament attached to a numbered disc (Scarratt and Elson, 1965).

The "spaghetti" or "sphyrion" tag is essentially an external tag, that is anchored internally either between the carapace and abdomen or elbow of the claw. By implanting the tag between the carapace and abdomen, a higher retention rate can be expected because this is where the lobster exits during molting. Improvements in these tags continued to be made and, after the successful laboratory experiments made by Hughes (reported by Anonymous, 1965, 1966), Scarratt (1970) and Cooper (1970) independently began using a vinyl tubing sphyrion tag instead of the numbered disc. With such a modification, Cooper (1970) reported an 88% retention rate for lobsters which had molted once, and the successful field tests of these tags (Cooper, 1970; Scarratt, 1970) spurred further, large-scale tagging studies in the United States and Canada; Krouse (1980a, 1980b), Stasko (1980), Miller et al. (1989) give reviews.

While it is impractical to review all tagging studies, a few will be summarized to show how the resulting data is applied to lobster management. Cooper and Uzmman (1971) and Uzmman et al. (1977) have documented the seasonal migrations of larger, deep-water lobsters from the continental slope and canyons to the shallow waters in the summer on Georges Bank. Uzmman et al. (1977) hypothesized that lobsters maintain an 8°–14°C temperature regime during their onshore migration in order to maintain growth, molting, and egg extrusion. Recently, this hypothesis has been confirmed by Chandler (1991) who conducted a series of in situ studies on outer Cape Cod, Mass., and recorded lobster size, sex, temperature range, and

behavior. From these data, she was able to estimate population structure. Other studies undertaken by Cooper (1970), Lund et al. (1973), and Ennis (1984) reported inshore movements to be minimal. Similar results have been reported for *H. gammarus* and *N. norvegicus* (Bennett et al., 1978; Chapman, 1980).

Besides the information on movements and behavior gained from such tagging studies, data in the form of growth, natural mortality, and fishing mortality has also been collected (Thomas, 1973; Smith, 1977; Krouse, 1981; Briggs and Mushacke, 1984; Miller et al., 1989) and used for lobster management (Northeast Marine Fisheries Board, 1978). The sphyrion tag has enabled researchers to gather significant life history data on the lobster in its natural environment; however, these data are limited to large juvenile and adult lobsters (>60 mm CL) (Krouse and Nutting, 1990a), which leaves gaps in information for smaller juveniles. Larger lobsters traditionally have been used for several reasons: 1) early researchers were more interested in older life stages, 2) until recently it was difficult to collect lobsters smaller than 40 mm CL, and 3) the sphyrion tag was thought to be unsuitable for smaller lobsters (Krouse and Nutting, 1990b).

Because the sphyrion tag was considered inappropriate for smaller lobsters, researchers began experimenting with lobsters < 60 mm CL to develop a satisfactory tagging technique. Bernstein and Campbell (1983) developed a miniaturized persistent back tag for lobsters 20–25 mm CL. Krouse and Nutting (1990b) modified the western rock lobster tag and reported retention rates of 100% on 30 lobsters of 25–39 mm CL. They recommended that this tag be used in movement and growth studies requiring observations over prolonged periods of time.

Another extremely successful method for tagging small lobsters was the Bergman-Jefferts “microtag.” Originally developed and used by Jefferets et al. (1963) for marking salmonids in enhancement experiments in the United States, the “microtag” was improved for use in lobsters. Saila and Flowers (reported in Anonymous, 1965) were

apparently the first to experiment with this type of tag, but their tag was made of 1.6 mm clear plastic tubing with a small wire insert. This was injected internally into the lobster with a hypodermic needle. Ennis (1972) successfully used internal tags for growth-per-molt studies of larger lobsters. More recently, a tag 0.25 mm in diameter and 1 mm long has become popular for use with lobsters as small as 9 mm CL (Wickins and Beard, 1984; Wickins et al., 1986; Cowan, 1999). Consequently, many enhancement programs for the lobster *H. gammarus* now use the “micro-tag” to evaluate the survival rates of hatchery-produced lobsters and compare these rates to wild stocks (Bannister et al., 1989; Cook et al., 1989; van der Meeren et al., 1990; Burton, 1992; Beard and Wickins, 1992; and Resource Enhancement section).

An even smaller tag (0.25 mm diameter by 0.5 mm long) has allowed the tagging of Stage V–VI postlarval lobsters (Burton, 1991, 1992). In the United States, Krouse and Nutting (1990a) successfully tagged *H. americanus* lobsters 12–24 mm CL with micro-tags 0.25 by 1 mm long. Their field and laboratory tests suggest that this tag is useful for the monitoring of movements, growth, and possibly mortality rates. Others have been experimenting with yet another type of tag called the polyethylene streamer tag. This tag was originally developed for shrimp, but has also been successfully applied to lobsters (Landsburg, 1991). The anchoring method of this streamer tag makes it possible to tag larval and postlarval lobsters (Landsburg¹¹). Finally, a rather unusual method for tagging lobsters actually records the number of molts. This method involves epidermal implants inserted into the abdominal haemocoel of the lobster. Each time the lobster molts, a layer of cuticle is formed. By counting these layers, the molt history can be ascertained (Shelton and Chapman, 1987, 1995). Lipofuscin granule content in the brain also holds a potential for aging cohorts of both *Homarus americanus* (Wahle et al., 1996) and its European counterpart, *Homarus gam-*

¹¹ Landsburg, W. 1991. Science Branch, P.O. Box 5030, Moncton, New Brunswick, Canada E1C 9B6. Personal commun., 3 Nov.

marus (Sheehy et al., 1996). The size and number of lipofuscin granules and the carapace length are significantly related to the age of the animal, such that it may be possible to determine the age of any lobster sometime in the future. Tagging experiments with smaller lobsters are important to determine the linkage between the numbers of postlarval benthic recruits with those eventually recruiting into the fishery.

Thus, lobster hatcheries, whether state-run or for experimental purposes only, have contributed to not only the “seeding” of larvae or postlarvae into coastal waters of New England states and European coasts, but also to much experimentation and description of the species’ natural history. Many of the early studies have had direct impacts on recent and current projects, providing not only the background for newer and supposedly more sophisticated work, but also the culturing techniques (scaled down) which supply the larvae and postlarvae necessary for this work. In nearly every case, the work of the past has been confirmed, rather than refuted. The articles published in various state fish commission bulletins have been cited and referred to for decades and are still being used. Herrick’s (1895, 1911) monographs, although sadly out of date, remain invaluable references for lobster biologists. An update to Herrick has been recently published, and contains several chapters devoted to the development and regulation of the fishery and aquaculture (Factor, 1995). Throughout all of these literature sources, the successes of the former and current hatcheries have kept alive the hope that lobsters might be someday commercially farmed.

Aquaculture Potential

Farming of the homarid lobster has been classified into several forms of “aquaculture:” Resource enhancement, product enhancement, full grow-out (Waddy, 1988; Edwards, 1989), and transplantation programs (Van Olst et al., 1980). More recently, another form has been suggested—that of a soft-shelled product (Wear, 1990).

Aquaculture involves manipulation of the natural population by culturing

(Van Olst et al., 1980), which is dependent on the ability to control and economically optimize all aspects of the biology and environment of the species cultured (Shleser, 1973). We present a review of these forms of aquaculture and the developments that have followed from their operations.

Resource Enhancement

Resource enhancement began over 100 years ago because of unenforced laws, increased demand, increased fishing effort, and declining lobster landings. As such, the homarid lobster received much attention from researchers on both sides of the Atlantic Ocean, and resource enhancement has been practiced continuously ever since.

The objective of these enhancement programs was to alleviate the high mortality associated with the pelagic stages in nature by releasing larval, postlarval, or juvenile lobsters. Several countries are currently engaged in this form of aquaculture, whether it be called "resource enhancement," "stock enhancement," or "seeding." Until recently, it was not clear if stock enhancement via the release of hatchery-reared lobsters provided any real benefit to the preservation of the species. Lack of tagging methods to distinguish hatchery-reared stock from those settling naturally prevented documentation of hatchery-reared lobster survival. However, several methods have been recently identified to distinguish hatchery-reared stock from those of the wild. These include the use of color morphs, genetic tags, hybrids, and micro-tags.

Color Morphs

John Hughes (1968a), of the Massachusetts State Lobster Hatchery, proposed using color morphs as natural tags to determine the survival and impact hatchery-reared lobsters had on the fishery. Later Anthony D'Agostino, of the New York Ocean Science Laboratory, incorporated Hughes' idea in his broodstock maintenance and development program using "blue" color morphs (Rattner, 1986; Irvine et al.⁵). Initially, the project was designed to develop a hatchery program for restocking New York's inshore wild lobster populations and to advance the technology and meth-

odology for lobster culture (Portersfield, 1982; Mead, 1989; Montauk Marine Science Institute, 1993). In addition to this "Blue Lobster Project," which is still in operation, D'Agostino was also responsible for releasing millions of Stage IV lobsters into Fort Pond Bay, Montauk, N.Y., during 1974–79. Though not yet reported in the literature, Goldfinger¹² states that the efficacy of this program is well-documented, but in unpublished data, and, as reported by the local fishermen, an increase in lobster numbers is evident. Goldfinger¹² asserts that "there is no question that seeding areas that have natural lobster habitat with Stage IV or V lobsters, will have a positive effect on future stock." At the Darling Marine Center in Walpole, Maine, Sam Chapman proposed a similar program to hatch, raise, feed, and release "blue" lobsters off the Maine coastline. His program was initially funded (Plante, 1989) and had the long-term goal of evaluating hatchery release programs (Plante, 1989; Irvine et al.⁵; see later section on culture work in Maine) and following year-to-year survivability in the wild, but it has since been terminated.

Permanent Genetic Tags

Genetic studies (Pressick, 1974; Hedgecock et al., 1975; Tracy et al., 1975; Hedgecock, 1977) revealed that there is one variable locus, phosphoglucomutase (PMG), in lobsters that could be used as a marker for distinguishing introduced lobsters from wild stock. An example of how this can be accomplished has been reported by Pressick (1974) and is explained as follows: lobsters from Woods Hole and Martha's Vineyard possess a slow moving allele (PMG¹⁰⁰) which is fixed, as there are no heterozygotes detected thus far in this population. In Maine, the lobster population has both a slow (PMG¹⁰⁰) and a fast (PMG¹⁰³) moving allele. The frequency of PMG¹⁰⁰ is around 0.16, which indicates that a homozygote for the rare allele could only be expected in about 3% of the individuals in Maine. By selecting and mating lobsters with the

rare alleles, the offspring will bear a natural tag—the numbers of progeny produced with these rare alleles will be greater than that expected in a natural population. This type of tag could also be used to monitor the survival rates and dispersion of hatchery-released lobsters (Pressick, 1974; Hedgecock et al., 1975; Tracy et al., 1975; Hand et al., 1977; Hedgecock, 1977).

Hybrids

Mating *H. americanus* and *H. gammarus* produces hybrids (Carlberg et al., 1978; Kittaka, 1984b) which possess the subrostral spine of *H. gammaurus*. They are therefore distinguishable from *H. americanus* (Wickins, 1983). However, this method may not be ecologically sound, as the release of nonindigenous species can have major effects on the natural communities into which they are released (Syslo, 1986).

Micro-tags

The micro-tag designed after Jefferets et al. (1963) has been used to create a binary coded-wire tag in several sizes. Researchers have successfully implanted tags of either 1 mm × 0.25 mm or 0.5 mm × 0.25 mm into the base of the fifth walking leg of the lobster and have documented a 90% retention rate (Wickins and Beard, 1984; Wickins et al., 1986; Krouse and Nutting; 1990a). This method is successfully used by several stock enhancement programs (see sections on Great Britain; Sea Fish Industry Authority, Scotland; North Western and North Wales Sea Fisheries Committee; Norway; and France).

Only two of the above methods are currently in use: micro-tags and color morphs. These methods will be presented with up-to-date information in the sections covering the individual stock enhancement programs using them.

Massachusetts

Until 1997, the Massachusetts State Lobster Hatchery and Research Station, Vineyard Haven, Martha's Vineyard, maintained the longest continuously running stock enhancement program in the world. Since 1949 this hatchery contributed substantially to the devel-

¹² Goldfinger, I. N. 1990. Marine Science Institute at Montauk, P.O. Box 820, Montauk, NY 11954. Personal commun., 24 July and 20 Aug.

opment of hatching techniques (Hughes and Matthiessen, 1962, 1967; Hughes, 1968a, b; Hughes et al., 1972; Hughes, 1972, 1973; Hughes et al., 1974; Schuur et al., 1976; Van Olst et al., 1980; Syslo and Hughes, 1981) which are still applied to hatchery programs worldwide. While the hatchery released approximately 500,000 Stage IV lobsters annually into the coastal waters of Massachusetts, its reseeded effort was terminated in January 1997 in order to allow the research station to focus more directly on its research goals. The station will conduct research on the incidence of multiple egg batch extrusion that occurs without mating, gather growth rates, and determine how much egg production can vary in the wild. Management then can use the information gathered to assess the health of the lobster stock (Estrella⁶).

Prior to its closure, the hatchery operations began with egg-bearing lobsters obtained from offshore fishermen by special permit. These females were placed into large fiberglass tanks, approximately 274 cm long × 91.5 cm wide × 30 cm high. During mid-May, when the water temperature rose to about 15°C, larvae hatched and were caught in a plastic screened box as the water drained from the tank through an overflow pipe. The larvae were then transferred to rearing tanks (kreisels) at stocking densities of about 3,000 Stage I larvae per kreisel. They were fed frozen adult brine shrimp, *Artemia salina*, and were reared for about 1 month until they molted into Stage IV. Once the Stage IV animals were removed for stocking, the kreisels were again stocked with Stage I larvae. Postlarvae were transported to an appropriate coastal area and were released by snorklers at the surface over a bottom that provided the maximum amount of shelter (Hughes and Matthiessen, 1962, 1967; Syslo⁷).

Besides stock enhancement, experiments on growth rates of juvenile lobsters, diets, color morphs, and polyculture techniques were conducted. Animals and technical advice were also provided to researchers (Syslo⁷), which contributed significantly to many experiments. Because the growth rate work was so voluminous and time was

spent entirely rearing and stocking, no new publications were written on diet or growth studies (Syslo⁷). However, experiments using various types of seaweeds have been published by Syslo and Hughes (1981) and have demonstrated that eelgrass, *Zostera marina*; Japanese weed, *Codium fragile*; Irish moss, *Chondrus crispus*; rockweed, *Fucus spiralis*; and kelp, *Laminaria* sp., can be used as a diet substitute for fish and may provide a less expensive nutritional supplementary diet which contributes to growth (Syslo and Hughes, 1981).

Experiments using color morphs have also been successful, particularly those of breeding; however, the rearing of larvae to a size of 40–50 mm CL has proven less successful since mortalities are higher than those with wild-type coloration. Based on the lower survivorship, color morphs may not provide reliable indicators of the survival rates of hatchery-stocked lobsters in the wild. Furthermore, since the brighter color morphs themselves may invite more predation, this part of the research was discontinued several years ago (Syslo⁷).

The illegal removal of eggs from berried (egg-bearing, or ovigerous) lobsters was a long-standing problem dating back to the early 1800's (Herrick, 1895). Several methods used for the removal of eggs were described by Templeman (1940d) and Hughes (1965) and included the use of a stiff brush, compressed air, and a high pressure hose. Hughes (1965) working at the Massachusetts State Lobster Hatchery developed a method for detecting scrubbed lobsters based on physiological and biological characteristics. This method was then enhanced by the use of biological stains (Karsson and Sisson, 1973). These techniques were useful for detecting the removal of eggs with the naked eye (Morejon, 1975). However, recent evidence suggested that fishermen were now dipping ovigerous lobsters in a chlorine bleach solution which dissolved all of the residual cement so that no obvious external signs could be seen by the naked eye. As a result, researchers from Massachusetts and Maine developed tests to determine if lobsters have been subjected to chlorine

bleach (Bullis and Syslo, 1996; Cogger and Bayer, 1996). Both of these tests indicate that lobsters exposed to chlorine bleach can be detected up to 12 days post-dipping.

After a visit to the hatchery in Massachusetts, Harvard Medical School researchers studying neurological disorders decided to start rearing their own larvae (Syslo, 1986). The Research Station aided their efforts by supplying ovigerous females at the New England Aquarium in Boston. The Research Station also assisted the Japanese Government by providing egg-bearing female lobsters for their research on the feasibility of introducing the American lobster, *H. americanus*, into their coastal waters in the hopes of stimulating a new fishery (Syslo, 1986; Kittaka, 1990; Syslo⁷). The Environmental Research Laboratory of the United States Environmental Protection Agency (EPA) in Narragansett, R.I., established a lobster rearing program in 1990 to hatch and rear larval lobsters employing similar techniques to those used at the Massachusetts hatchery. In 1992 they had over 5,000 lobsters in culture which were used solely for environmental testing purposes (Johnson¹³); however, they too have since terminated their culture program.

Maine

Bayer (1982) submitted a feasibility study for a hatchery-release program to the Department of Marine Resources, and in 1986 five lobster hatcheries were established at Cutler, Walpole, Stonington, Five Islands, and Bar Harbor, Maine. The first two hatcheries were funded primarily by the lobster industry, but the towns themselves, local fishermen, and the University of Maine all contributed funds, equipment, and time to these programs. Stonington and Five Islands hatcheries were funded and operated by the local fishermen on a volunteer basis (Plante, 1986). The Bar Harbor hatchery is funded and operated by the Bar Harbor and Southwest Bar Harbor Oceanariums and tourist admissions (Schreiber, 1998). Although Five Islands ceased operation

¹³ Johnson, M. W. 1991. Environmental Protection Agency, Environmental Research Laboratory, 22 Tarzwell Drive, Narragansett, RI 02882. Personal commun., 17 May.

in 1988, three of the remaining hatcheries released Stage IV postlarvae until 1991 in the following numbers: 544,681 (Cutler); about 20,000–30,000 (Stonington); and between 93,000 and 95,000 Stage IV and V lobsters, including 8,000 “blue” color morph lobsters (Walpole) (Chapman¹⁴).

Operations at Cutler and Walpole consisted of similar procedures for production of Stage IV postlarval lobsters (Plante, 1986), so, with this in mind, only Cutler will be reviewed. Based on Beal’s (1988) work at the University of Maine at Machias, the variables influencing larval survival were identified. These included food type, aeration rate, and initial stocking density, and the methodology used at Cutler took them into account (Fitzhenry et al., 1989). Broodstock (berried females) were obtained from the local waters off Cutler, Maine, by specially licensed fishermen, but were also obtained from as far away as Long Island Sound, N.Y., in an attempt to extend larval production seasons. Because local broodstock was only available during the months of June through October, it was hoped that these warmer-water, egg-bearing lobsters would hatch out sooner, thereby extending the season. However, observations from experiments revealed that after adjustment to the cold waters of Maine, the New York lobsters took longer to hatch (Fitzhenry et al., 1988). By using local lobsters and applying the techniques employed at the Biological Station in St. Andrew’s, New Brunswick (Waddy and Aiken (1984a) provide details), Cutler was able to successfully expand its production season for about 1 month (Fitzhenry et al., 1989).

Broodstock were maintained in two separate tanks: an 800 l tank for individuals 2–4 weeks away from hatching and a three-tiered tank for females currently releasing larvae (Fitzhenry et al., 1988). For Stage IV lobster production, Cutler used 10 (400 l) conically shaped tanks supplied with aerated seawater. The aeration not only oxygenated the seawater but also provided vigor-

ous water circulation to minimize larval interactions which could otherwise lead to cannibalism. The entire volume of seawater was replaced every 48 hours by water pumped from the harbor, ensuring a high level of fresh seawater at all times (Fitzhenry et al., 1989).

Once the larvae hatched, they were immediately collected with a small aquarium net, weighed (for counting purposes), and added to a food-enriched conical tank (Fitzhenry et al., 1988). To minimize larval interactions, initial stocking density was low, at about 40 individuals/liter. Additionally, a high rate of aeration and a high concentration of brine shrimp, *Artemia salina* (about 600–1,000 per larvae), was provided to prevent cannibalism (Beal, 1988; Fitzhenry et al., 1989). Unlike most hatchery operations, Cutler fed both algae and brine shrimp to larval lobsters. This method was first employed by Sam Chapman at the Darling Marine Center, Walpole Hatchery (Fitzhenry et al., 1986). The basic formula consisted of about 290 l of warm seawater, 100 l of cultured algae, *Isochrysis galbana*, and about 50 ml of brine shrimp eggs. Supplying brine shrimp with a nutritionally balanced food source thus resulted in a superior food item for the dietary requirements of larvae throughout all their rearing stages (Fitzhenry et al., 1989). The algae was also produced at Cutler under a process described by Fitzhenry et al. (1988).

During the course of rearing the larvae, temperature was maintained at an optimal level of 20°C so that Stage IV was reached in about 11 days (Table 3). Approximate cost to produce Stage IV lobsters is listed in Table 6. The number of females needed to obtain the required amount of Stage IV larvae is presented in Table 7; however, caution should be used when using this table because of the indices being used. Although the method described by Perkins (1971) was used to calculate the number of eggs per female lobster and can be used as a rough guide to estimate how many lobsters are needed for a production season, it is not very accurate since the number of eggs per female is always less than predicted. These losses are usually due to eggs being dropped

Table 6.—Cost to produce Stage IV postlarval lobsters. (adapted from Fitzhenry et al., 1986.)

Percent survivorship	Cost ¹ per individual stage IV lobster	Percent survivorship	Cost ¹ per individual stage IV lobster
100	2.1	40	5.2
90	2.3	30	6.9
80	2.6	20	10.4
70	3.0	10	20.8
60	3.5	5	41.7
50	4.2		

¹ Cost in cents.

Table 7.—Number of Stage IV postlarvae produced from egg-bearing females; adapted from Fitzhenry et al. (1986) with estimated number of stage IV postlarvae at 80% survival rate.

Carapace length (mm)	Estimated number of:			
	Eggs per female	Egg-bearing females	Total eggs	Stage IV lobsters
80	6,704	10	67,040	53,632
85	8,119	8	64,952	51,962
90	9,723	7	68,061	54,449
95	11,534	6	69,204	55,363
100	13,561	6	81,366	65,093
105	15,819	4	63,276	50,621
110	18,322	4	73,288	58,630
115	21,082	3	63,246	50,597
120	24,114	3	72,342	57,874
125	27,430	3	82,290	65,832

when the lobster is transferred from the trap to the holding tank or when the lobsterman transfers the lobster to the hatchery.

For an accurate estimation of stocking densities, Cutler established a reliable technique to count both Stage I and Stage IV larvae via a mass-to-count ratio. The equipment needed to do this consists of a small 7.62 cm diameter PVC pipe that is 12.7 cm deep and has a 175 μm mesh screen epoxied to the bottom. Larvae were placed into this tube and weighed. Their number was estimated by the equations below:

$$\text{No. of Stage I larvae} = \frac{\text{weight (gm)} - 0.069}{0.00633} \quad (1)$$

or, if using postlarvae,

$$\text{No. of Stage IV larvae} = \frac{\text{weight (gm)} - 0.09}{0.03832} \quad (2)$$

This system can be used at any hatchery, and Fitzhenry et al. (1989) give full details.

Release of Stage IV lobsters was made in tidal fronts near shallow subtidal eelgrass or kelp beds. The lobsters were released through a large funnel that had a 5 to 6 foot weighted exten-

¹⁴ Chapman, S. 1991. University of Maine at Orono, Dep. Oceanogr., Ira C. Darling Mar. Cent., Walpole, ME 04573. Personal commun., 25 Oct.

sion attachment mounted to a tapered snout (Fitzhenry et al., 1988). Release occurred at dusk (to reduce losses to visual predators) on a rising tide. Other experiments were being conducted to test the hypothesis that survival success increased in cobble areas compared with an unvegetated mud area (Fitzhenry et al., 1989).

Besides the goal of enhancing natural stocks, the Maine hatcheries were interested in the development of "blue" color morph lobsters as biological tags. A long-term project was initiated in 1987 by researchers from the Darling Marine Center, Walpole Hatchery, and the University of Maine at Orono and Machias (Irvine et al.⁵). However, it was unclear if "blue" lobsters would survive or behave in a manner similar to wild-type individuals (Irvine et al.⁵). Several researchers speculated that "blue" lobsters might be more easily detected by predatory fish and thus suffer higher mortalities (Portersfield, 1982; Fitzhenry et al., 1986; Plante, 1989; Syslo⁷).

Several pilot-scale experiments were conducted in 1988 and 1989 to determine the survival and growth of hatchery-reared "blue" postlarvae released in the natural environment. In 1988, 5,600–6,000 Stage IV and V "blue" lobsters were released in a 20 × 100 m cobble patch at Damariscove Island, Maine. A day after release, densities were about 10 times lower than expected, had all of the lobsters recruited into the cobble patch. Curiously, 1 year later, densities were about the same as the day after the initial release. The initial losses have been assumed to be due to predation and dispersion in the water column (Steneck et al.¹⁵). In 1989, 70 "blue" lobsters ranging in sizes from 12 to 14 mm CL were released. Within 1 week their numbers decreased about 40% to > 2/m², but the population density remained constant at that level for over 10 weeks (Steneck et al.¹⁵). By 1992, several of the blue lobsters had

grown to trapable sizes and were captured (Bulkeley, 1993). Wahle (1991a) and Wahle and Incze (1997) also placed hatchery-reared "blue" lobsters onto artificial cobble plots on a featureless sand-bottom cove in Maine and monitored the growth and densities of the juvenile lobsters over time.

Experiments on the behavioral traits (swimming, burrowing, walking, and lack of activity) of "blue" lobsters were also conducted using six different substrates: sand, eelgrass over sand, cobble over sand, pebbles over sand, mud, and eelgrass over mud (Irvine et al.⁵). All lobsters used for this study were postlarvae and had carapace lengths between 4.0 and 6.8 mm. No behavioral differences were detected between the "blue" and normal (control) lobsters (Beal et al., 1998; Irvine et al.⁵). However, smaller lobsters (4.0–4.9 mm CL) swam more often over sand and swam least often over cobble than those of 6.0–6.8 mm CL. Conversely, larger postlarval lobsters burrowed more readily than small ones, mainly on the eelgrass over mud substrates. Walking and lack of activity in this study corresponded to the previous observations of Botero and Atema (1982) and Hudon (1987) in that lobsters 4.0–4.9 mm CL spent more time walking. These results tend to support the hypothesis that younger and smaller postlarvae use their energy searching for an appropriate substrate rather than for growth (Botero and Atema, 1982; Hudon, 1987; Cobb et al., 1989a; Anonymous, 1991c; Irvine et al.⁵).

Other studies have been directed toward placing cobble (10–125 cm diameter) in areas where recruitment exists but habitat is limited. Population densities within these cobble patches averaged 6 lobsters/m² compared to 0.1 lobsters/m² in the adjacent sand area (Steneck et al.¹⁵). Thus, it would seem that lobster populations could be further augmented by adding cobble to shallow coastal areas having good postlarval supply but poor recruitment site characteristics. Based upon field measurements of similar naturally occurring densities of 3–6 early benthic phase lobsters/m² and about 0.5–1 adolescent phase lobsters/m², habitat enhance-

ment could sustain 30–60,000 lobsters annually (conservatively valued at over \$100,000 annually) (Steneck et al.¹⁵).

Currently, although Maine's lobster hatcheries have provided information (e.g. rearing and hatching techniques), only one lobster hatchery remains in operation at the Mt. Desert Oceanarium, Bar Harbor. Hatchery techniques are modeled after Cutler and have allowed the release of 40,000 postlarval lobsters to Bar Harbor, Winter Harbor, Northeast Harbor, Seal Cove, Southwest Harbor, and Islesford, Maine. Besides reseeding efforts, this hatchery provides postlarval lobsters for research. At the Bigelow Laboratory for Ocean Sciences, Dr. Rick Wahle has requested 10,000 larvae to develop a tracking system (Schreiber, 1998).

Great Britain

Homarus gammarus natural stock enhancement is being tested by three groups in the United Kingdom. Experiments were initiated by scientists from the Ministry of Agriculture, Fisheries, and Food (MAFF) directorate of fisheries research at Burnham, Conway, and Lowestoft (Richards and Wickins, 1979). Following MAFF's methodology, trials began by two other groups: Sea Fish Industry Authority (SFIA) in Scotland, and North Western and North Wales Sea Fisheries Committee (NWNW-SFC) in Wales (Anonymous, 1991a; Burton, 1992; Cook et al., 1989). The latter two programs are summarized separately.

At MAFF, ovigerous females are obtained from the fishery for larvae production, and a 900 l recirculating system maintains the egg-bearing lobsters (Richards and Wickins, 1979). Larvae are reared in 100 l cone-shaped polyethylene hoppers (originally designed to hold agricultural feed). Ten such hoppers are formed into a recirculating rearing unit, and each is stocked with 2,000 larvae that are hatched within a 2-day period. A second system contains ten 40 l fiberglass tanks similar to the first system, each stocked with 1,500 larvae (Beard and Wickins, 1992).

Larvae are fed twice daily with frozen mysid shrimp, *Neomysis* sp., and a supplement of *Artemia* nauplii 3 times per

¹⁵ Steneck, R. S., R. Wahle, D. Dow, E. Blackmore, and B. F. Beal. 1990. Maine lobster enhancement program, phase 1 and 2. A proposal to the Maine Aquaculture Innovation Center. Unpubl. rep., 19 p. Avail. from Robert Steneck, Univ. Maine, Ira C. Darling Mar. Cent., Walpole, ME 04573.

week. It takes 9–26 days for the larvae to reach Stage IV (postlarvae) with an average of 16 days at a temperature of 20°C (Beard et al., 1985). Once at Stage IV, the postlarvae are removed by a hand net, counted, and placed into individual compartments. The grow-out unit consists of a primary system of 6,212 l capacity with 5 rows each with 4 rearing troughs (2.94 m long × 0.51 m wide × 0.15 m high). The second system, which has a 12,116 l capacity, contains 4 rows, each with 4 troughs. Each trough contains 80 individual compartments (5 cm long × 5 cm long × 10 cm high) (Beard and Wickins, 1992). Postlarvae are fed twice daily with 2–6 pieces of mussel in the morning and 6–9 mysid shrimp in the afternoon.

Reared at temperatures of 18°–21°C, Stages X to XII (about 11–15 mm CL) are reached in about 3 months (Beard et al., 1985). These juvenile lobsters are then tagged with a binary coded micro-tag (1 mm long × 0.25 mm diameter) which is inserted at the base of the fifth walking leg (Fig. 16). Tag retention through several molts is about 90% (Wickins et al., 1986). Marked lobsters are detected by passing the whole lobster through an instrument which emits an audible sound if the tag is present, and each year from 1988 to 1994, an average of 10,000 lobsters were tested for the presence of these tags. Full details on experiments and techniques used at MAFF are given by Richards and Wickins (1979), Howard (1982, 1988), Beard et al. (1985), Bannister and Howard (1991), Addison and Bannister (1994), and Bannister (1998). Beard and Wickins (1992) provide a comprehensive report on techniques for mass culture, tagging procedures, transportation methods to release sites, release techniques, number of personnel needed, and time required for each procedure.

During MAFF's experimental lobster enhancement trials, several studies assessed the reaction of hatchery-reared lobsters to substrates and water currents in an attempt to determine the proper location for the release of lobsters. Howard and Bennett (1979) reported that postlarval lobsters (8 mm CL) readily burrowed into fine cohesive mud

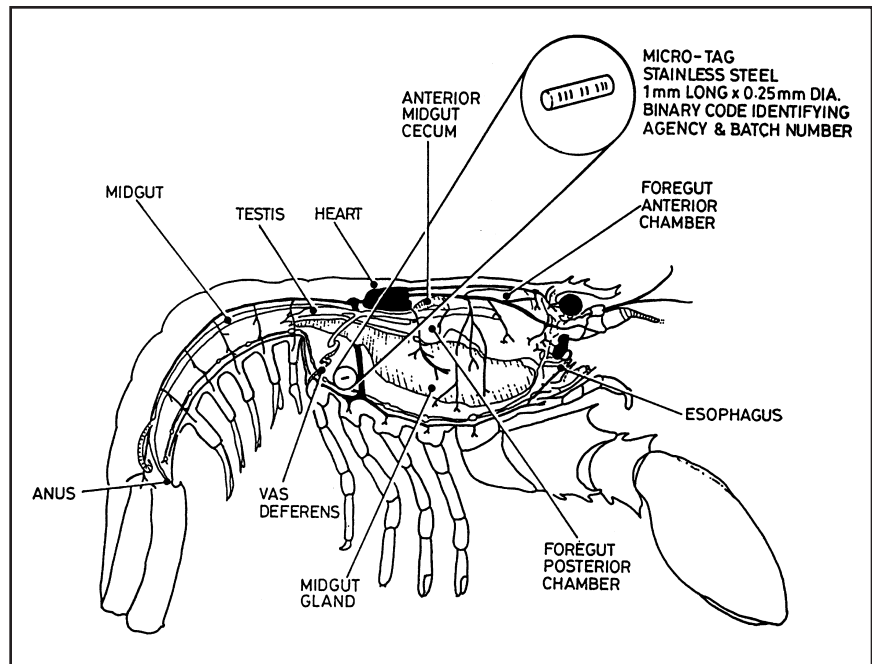


Figure 16.—Diagram of juvenile lobster showing position of microtag at the base of the fifth walking leg. From Burton (1992). Used with permission.

or selected coarse substrates (stones 7–20 mm diameter) which offered suitable crevices. In experimental releases, lobsters liberated at the surface took 5–10 minutes to reach the bottom (16 m depth) (Howard, 1983). If released at the surface, these lobsters would be displaced from the suitable site; however, 90% of the lobsters released at a carefully selected site with a suitable bottom found shelter in 2 minutes (Howard, 1982).

Furthermore, water velocities on the bottom significantly affect the ability of lobsters to move: large lobsters (15 cm TL) were exhausted by moderate currents of 30 cm/sec, while smaller lobsters (5 cm TL) could rest in the lee of small obstructions to avoid such currents (Howard and Nunny, 1983). Because of this ability to avoid currents and the ability to find shelter in 2 minutes, Howard concluded that 80% of hatchery-reared stock released into suitable substrates had as much chance of survival as their wild counterparts (Howard, 1982).

Using the above methodology, MAFF released about 49,000 hatchery-reared Stage XII lobsters at 80 different reef

sites between 1983 and 1988 (Anonymous, 1995). Each lobster was tagged with a coded micro-tag and was released by MAFF divers onto various selected habitat patches in Bridlington Bay on the east coast of England (Bannister et al., 1991). Results from these releases have been very encouraging, with hundreds of returns being documented: 26 in 1988 (Bannister et al., 1989), 110 in 1989 (Bannister et al., 1990), 218 in 1990 (Bannister et al., 1991), 115 in 1991 (Burton, 1993), 152 in 1992 (Addison and Bannister, 1994), and 32 in 1993 (Cook, 1995) for a total of 653 recaptures, ranging in age from 3 to 9 years (Anonymous, 1995; Table 8). Most were recaptured from areas clustered within 5 km of their initial release sites (Anonymous, 1995). A large proportion of these recaptured lobsters were of legal size and ten were egg-bearing females; thus, there was no doubt that hatchery-reared stock were contributing to the natural stock (Bannister et al., 1989, 1998).

Estimated returns on investment for stocked lobsters are encouraging. For example, if mortality is assumed at 10% per annum, 40–50% of those released

Table 8.—Recaptures of hatchery-reared lobsters released in the United Kingdom from MAFF and NWNW SFC hatcheries (source: Burton (1993), Cook (1995), and Bannister (1998)).

Hatchery and year of release	Number released	Numbers recaptured						
		1988	1989	1990	1991	1992	1993 ²	1994 ²
MAFF ³								
1983	2,390	14 (65-82)	19 (78-96)	6 (88-96)	0	0	0	
1984	8,616	12 (52-78)	67 (54-95)	97 (67-100)	25 (85-101)	14 (87-108)	0	
1985	7,979	0	24 (70-92)	112 (83-114)	21 (81-106)	5 (86-97)	0	
1986	11,562	0	0	1 (88)	28 (85-96)	39 (85-100)	5	
1987	12,629	0	0	2 (76, 82)	41 (70-102)	72 (85-108)	20	
1988	5,952		0	0	0	22 (84-108)	7	
NWNW/SFC ⁴								
1984	1,250	0	0	33 (87-102)	6 (87-100)	3 (113) ⁵	0	0
1985	3,750	5 (51-58)	0 (84-99)	67 (84-106)	74 (84-102)	31 (84-102)	11 (96) ⁵	0
1986	2,438	0	3 (56-58)	5 (86-96)	28 (85-105)	26 (85-108)	2 (96) ⁵	0
1987 ⁶	5,079	0	0	0	2 (88, 90)	36 (83-96)	23 (93) ⁵	0
1988	6,706		0	0	3 (85-86)	40 (84-101)	44 (90) ⁵	11 (95) ⁵

¹ Numbers in parentheses represent size in m CL.

² Data still being processed.

³ Ministry of Agriculture, Fisheries, and Food.

⁴ North Western and North Wales Sea Fisheries Committee.

⁵ Mean CL size of lobsters recaptured.

⁶ Animals released in December 1986 had the same code as those released in 1987.

could reach market size in about 5 years. From those, 70–80% would be available for capture by the fishery indicating a possible tenfold increase in value (Wickins, 1983). Furthermore, with survivors contributing their own progeny to the wild population, the return on investment could be compounded (Aiken and Waddy, 1989). At 15 pence (about US\$0.30) to produce a lobster the size of 3 cm, an operation could break even with only a 3% survival rate (Anonymous, 1982).

Optimistically, if proper procedures are used during rearing and release operations, no less than 42% of those lobsters being released would reach commercial size (Anonymous, 1982). With these predictions and the use of Syslo's economic impact statement (Table 4), the return on investment could be very high. For example, if 500,000 postlarval lobsters were released, and an assumed 42% (as noted above) survived to reach commercial size, then the 290,000 (42% of 500,000) animals would, at a value of \$3.14/pound, represent a potential \$910,600 to lobstermen. By multiplying this potential \$910,600

by the 4.5 economic multiplier (which represents the worth of the lobster as it is sold and resold relative to the personnel who are employed to hold, ship, and prepare lobsters), a total economic value of \$4,097,700 would be realized.

North Western and North Wales Sea Fisheries Committee

Following the techniques used by MAFF, a hatchery was built at the University College of North Wales, Menai Bridge, and lobsters are being released off Aberystwyth, Cardigan Bay, North Wales (Bannister et al., 1989). Production began in 1984, with a maximum rearing capacity of 3,072 postlarval lobsters. From 1984 through 1988, 19,237 postlarvae were reared and released (number adjusted after tag loss). Before 1988, the smallest lobster released was 10 mm CL, with the mean size of each batch at 12–14 mm CL. In 1988, released lobsters ranged from 6 to 45 mm CL (Cook et al., 1989). Five lobsters were recaptured in 1988, ranging in size from 51 to 58 mm CL, and all were from the 1985 releases (Cook et al., 1989).

In 1990 the first lobsters of commercial size were screened to determine whether the tag was present; 105 tagged lobsters were recovered. Of these, 33 were from the 1984 cohort and ranged in size from 87 to 102 mm CL (with a mean size of 93.24 mm CL), while 67 were from the 1985 cohort and ranged in size from 84 to 99 mm CL (with a mean size of 89 mm CL). In addition, five lobsters were captured from the 1986 cohort, ranging in size from 86 to 96 mm CL (mean of 90.2 mm CL) (Table 8) (Cook, 1990). During the recapture experiments of 1991, some lobsters gave off a false positive response when passed through the machine. Dissection revealed that these lobsters were not tagged, but their tissues contained small particles of rusted metal which were picked up by the extremely sensitive detection machine. The source of these rust particles remains unknown (Cook, 1992). In total, 453 lobsters have been recaptured, representing a recapture rate of 2.4%. Of these lobsters, 445 were of a legal, commercial size which varied from 85 mm to 103 mm CL (Cook, 1995). The sex ratio of the recaptures was skewed towards females in approximately a two to one ratio (288 females versus 157 males), but only 20 out of 195 females examined were ovigerous. These were slightly larger than nonovigerous females (93 mm vs. 90 mm CL) (Cook, 1995). Burton (1993), Addison and Bannister (1994), Cook (1995), and Bannister (1998) provide comprehensive updates on the United Kingdom's stock enhancement program.

Scotland

Lobsters are also reared at the SFIA Marine Farming Unit, Ardtoe, Argyll, West Scotland. The Ardtoe hatchery was established to provide up to 10,000 juvenile lobsters/year in two batches. Berried females are obtained from the wild and held in troughs 3 m long × 1 m wide × 0.6 m high (Fig. 17). Once the eggs hatch, larvae are collected, counted, and transferred to a rearing system where they are held in 80 l polypropylene hoppers (Fig. 18, 19) and fed on frozen mysid shrimp and chopped mussels. At 16°–17°C larvae reach Stage

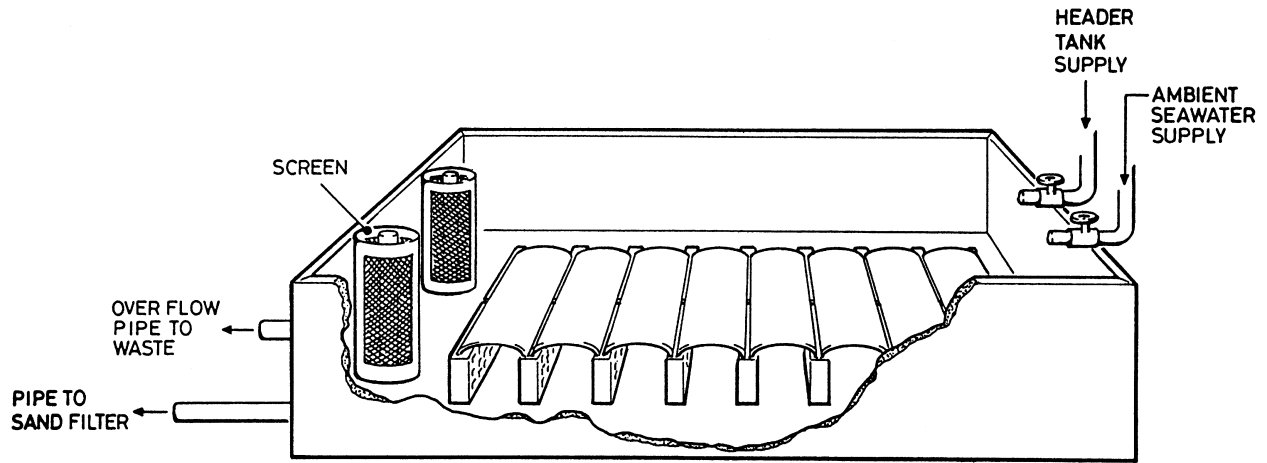


Figure 17.—Broodstock fiberglass trough 3 m long \times 1 m wide \times 0.6 m high. PVC is used for all pipe and valve work. 2 mm mesh screens cover the 15 cm diameter PVC frames on the outflow and overflow pipes. Each broodstock trough houses 15 egg-bearing females. From Burton (1992). Used with permission.

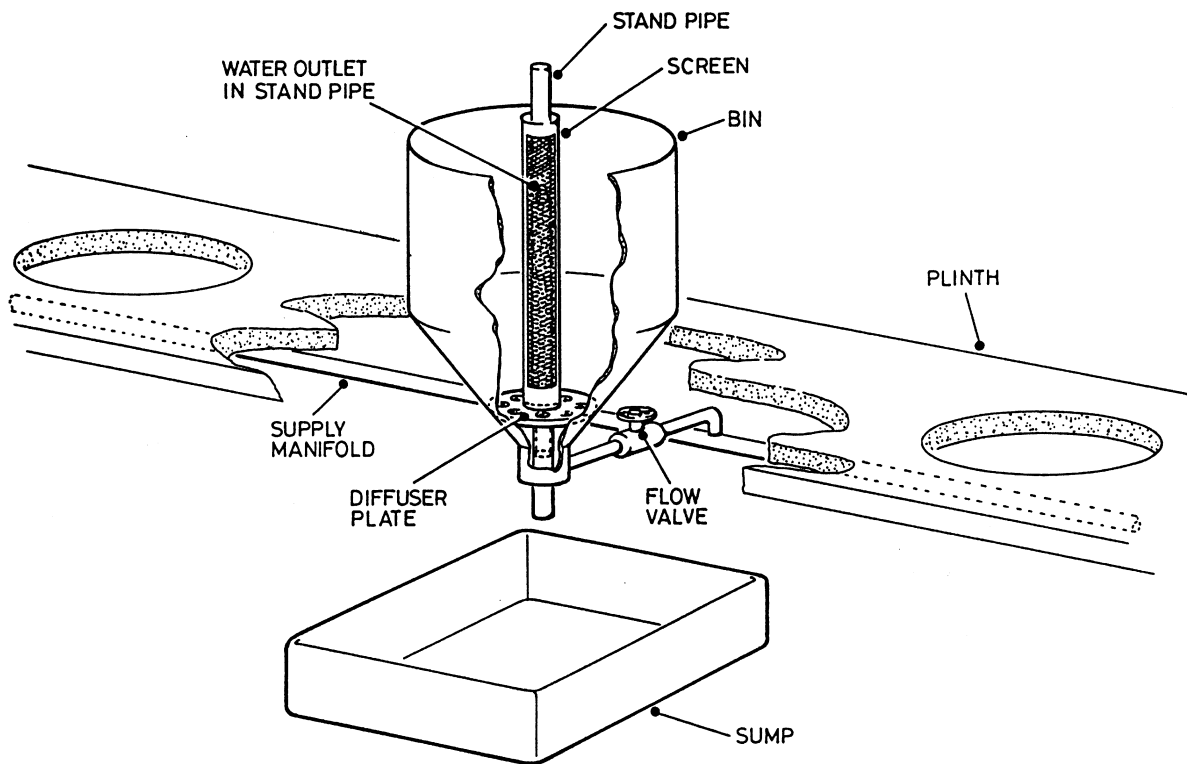


Figure 18.—Larval kreisels made from 80 l polypropylene hoppers, originally designed for agricultural purposes. The diffuser plate is made of PVC with holes drilled around the perimeter to provide water agitation. The 15 mm diameter standpipe is screened with 2 mm mesh screening. From Burton (1992). Used with permission.

IV in 12–18 days, but survival is somewhat low (5–30%, averaging 14%) (Burton, 1992). At Stage IV, the post-larvae are transferred to one of two sys-

tems for rearing to Stage XII: one is a horizontal trough system, as described above (Fig. 19) and the other is a vertical stack (Fig. 20).

Both systems house the lobsters individually (Burton, 1992; Fig. 21) and they are fed manually or with an automatic feeding system (Wickins et al.,

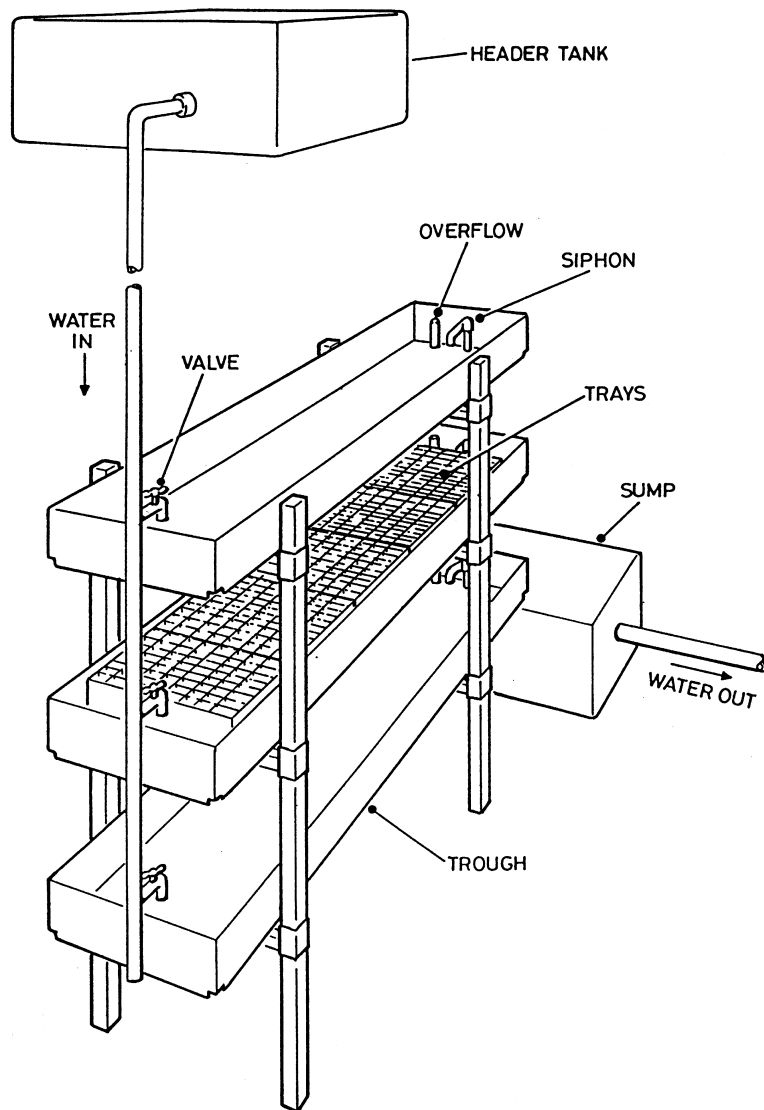


Figure 19.—Trough on-growing system for juvenile lobsters. The fiberglass trough's inner dimensions are 254 cm long \times 57 cm wide \times 15 cm high. The siphon produces a 25 mm rise and fall of the water level every 15 minutes. From Burton (1992). Used with permission.

1987) which can dispense mysid shrimp or pelleted diets. During the growth process, the diet is similar to that of the larvae, but it may be supplemented with *Artemia* (Burton, 1992). Survival from Stage IV to Stage XII is about 80%.

Two systems are used to release the lobsters: a stacked tray (Fig. 22 and 23) and a pipe release (Fig. 24). Both methods are designed to convey the microtagged Stage XII juveniles to the selected substrate (methodology after MAFF: Burton, 1992) in the best pos-

sible condition and to minimize predation during release.

SFIA began releasing lobsters at Ardtoe and Scapa Flow in 1984, and lobsters have been captured ever since (Anonymous, 1991a). An extensive study conducted by divers in 1985 recovered 5 microtagged lobsters (Walker, 1986). However, 1989 saw the first recoveries of market-sized lobsters with 6 having carapace lengths of up to 100 mm (Burton, 1992). The 1990 recoveries were more successful with 105 mar-

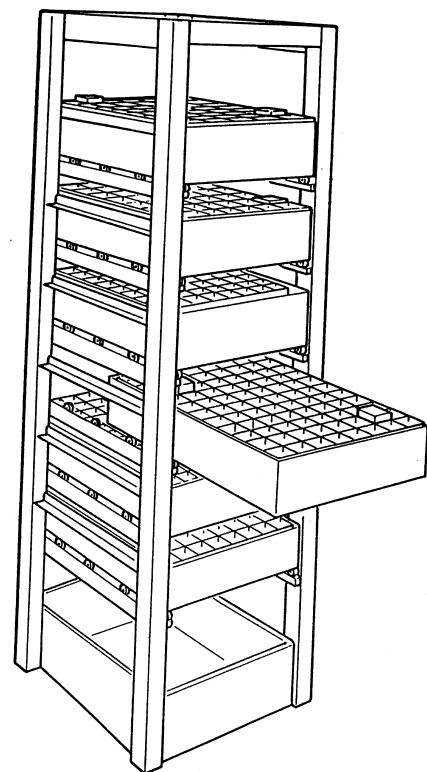


Figure 20.—Vertical stacking system made of frames of aluminum and trays 63 cm long \times 44 cm wide \times 13 cm high. Rollers are used to make the drawers holding the trays move backwards and forwards in the frame during feeding times. From Burton (1992). Used with permission.

ket-sized lobsters, ranging in size from 85 to 102 mm CL. Berried females and males with mature testes have been found, confirming that hatchery-reared stock will mature and reproduce in the wild. Samplings indicate that these recaptures are from the 1984–85 cohorts (Table 9) (Anonymous, 1991b; Burton, 1991, 1992).

In 1990 releases of Stage V juveniles began using a smaller microtag (0.5 mm long \times 0.25 mm diameter). For the first release, 1,200 Stage V–VI lobsters were tagged, with 1,170 surviving 3 days later (77.5%). Unfortunately, in subsequent batches a higher mortality was experienced in lobsters of less than 6 mm CL; however, this mortality has been subsequently stabilized (Burton, 1991). Tag retention is 96% after animals have molted at least once. No data

from these releases is available thus far (Cook, 1995).

Beginning in the summer of 1995, a pilot-scale lobster hatchery was established on the Scalloway Islands, Shetland to assess the practicality of producing juvenile lobsters for stock enhancement (Watt and Arthur, 1996). Egg-bearing females, obtained from local fishermen, were held first communally in a large tank and then were separated just prior to their eggs hatching. The females were fed on whitefish, salmon, and crab meat 2–3 times weekly.

Despite these holding conditions, 500 g females, known to produce ~700 eggs, only produced about 500 larvae, which were transferred to three different kinds of larval rearing systems: 1) an 80 l conical tank with air stones at the bottom for water agitation, 2) an 80 l conical tank with a diffuser plate (similar to that in Fig. 18) for water agitation, and 3) individual trays suspended in water. Only 10% of the larvae in both conical tank arrangements survived; none of the larvae survived when housed individually in submerged trays (Watt and Arthur, 1996).

Stage IV postlarvae were produced in 8–12 days and were then transferred to ongrowing, individual bins. They were reared only to Stage V, with a 77% survival rate, and then were released via a 3-inch flexible pipe in a design similar to that diagrammed in Fig. 24. In 1995, 1,000 juveniles were released in this manner, but the hatchery was expected to expand within the next couple of years to produce over 30,000 juveniles per year (Watt and Arthur, 1996).

Ireland

Recently, Ireland has become interested in the hatching and release of *Homarus gammarus* juveniles. The first prototype lobster hatchery in the country was constructed at the University College Galway's Shellfish Laboratory in Carna, Galway (Grogan, 1997). Here they modelled their entire project after a Cutler, Maine hatchery program (Browne and Mercer, 1998). Female lobsters are maintained in barrels of circulating seawater. Larvae are then transferred to special tanks at a density of 1,000 individuals per tank and are maintained at

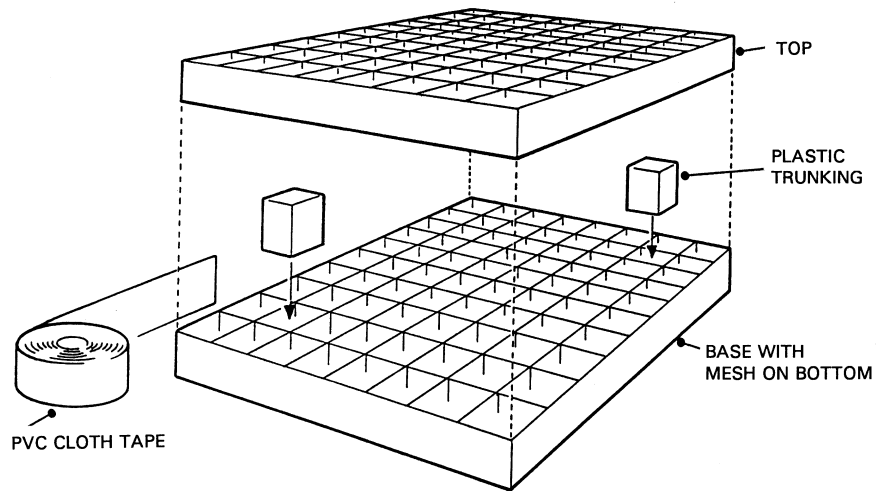


Figure 21.—Exploded diagram of tray construction for the stacking and transportation systems. The polystyrene trays, 540 mm long × 432 mm wide × 44 mm high, house 80 lobsters individually. In the stacking system, two trays are placed into each drawer, with the upper tray having a bottom made of 2 mm mesh. The trays are taped together. From Burton (1992). Used with permission.

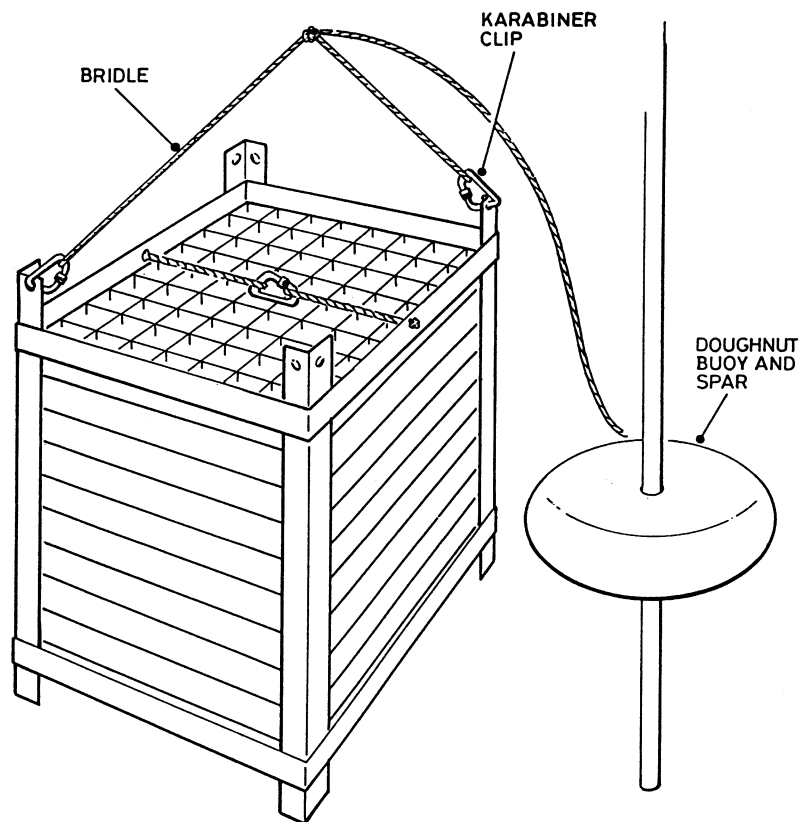


Figure 22.—Arrangement of trays in a frame. These stacks are taken to the sea by divers for release of tagged juveniles. From Burton (1992). Used with permission.

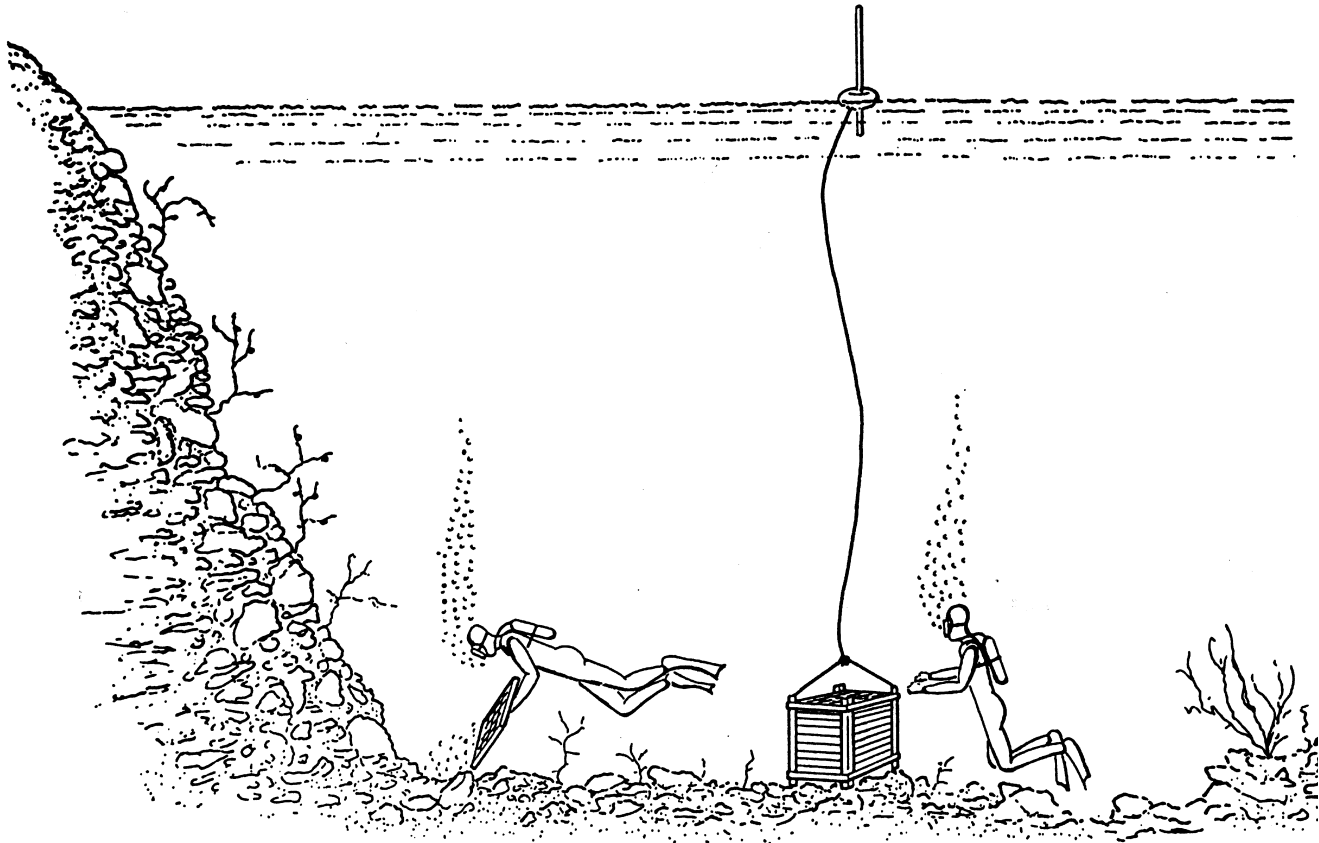


Figure 23.—Diagram of how lobsters are released by divers using the stack method. From Burton (1992). Used with permission.

Table 9.—Recaptures of hatchery-reared lobsters released from SFIA Ardtoe and Scapa Flow hatcheries (source: Burton (1993) and Anonymous (1995)).

Hatchery and year of release	Number released	Numbers recaptured ¹									
		1985	1986	1987	1988	1989	1990	1991	1992	1993	
SFIA ² /Ardtoe											
1984	451	2 (31, 41)	2 (45, 59)	3 (53-57)	9 (43-84)	8 (71-102)	1 (94)	0			
1985	1,268		0		2 (54, 70)	6 (56-76)	5 (76-86)	1 (76)			
1986	513			0		0	0	0			
1987	553			0	1 (56)	4 (48-60)	8 (55-63)	4 (59-84)	1 (65)		
1990	259							0			1 ³
SFIA ² /Scapa Flow											
1984	4,469	3 (18-22)	n.d.	18 (52-56)	3 (49-55)	16 (56-100)	84 (81-102)	68 (84-118)	23 ³		1 ³
1985	3,800		0	0	0	1 (67)	10 (82-102)	3 (84-87)	12 ³		1 ³
1986	2,356			0	0	0	0	0	5 ³		
1987	3,610				0	0	0	1 (85)	37 ³		5 ³
1988	2,260					0	0	0	8 ³		4 ³
1989	3,025						0	0	0		1 ³

¹ numbers in parentheses represent size in mm CL.

² Sea Fish Industry Authority.

³ CL data not available.

⁴ n.d. No data available

temperatures of 21°C (Grogan, 1997). Larvae are fed a mixture of algae and brine shrimp. Algae are cultivated at

Carne while the brine shrimp eggs are imported from Great Salt Lakes in Utah, USA. Approximately two months after

the lobsters reach Stage IV, they are released. Methods of release involve transporting the lobsters individually in plastic trays covered with tissue paper. Each tray is then lowered in a lobster pot usually on a rocky bottom. The tissue paper dissolves within 20 minutes after it has entered the seawater, and the lobsters can then escape into the rocks. The pots keep predators from attacking the lobsters during this time. Currently, the hatchery can produce over 30,000 juvenile lobsters per year and will continue to do so for about seven years (Grogan, 1997; Browne and Mercer, 1998).

Norway

During the early 1980's the worlds largest "commercial" lobster hatchery was constructed at Kyrksøterøra, south of Trondheim, Norway (Schjetne, 1987; Tveite and Grimsen, 1990), in response to the collapse of the Norwegian lobster fishery, whose landings fell from 500 t

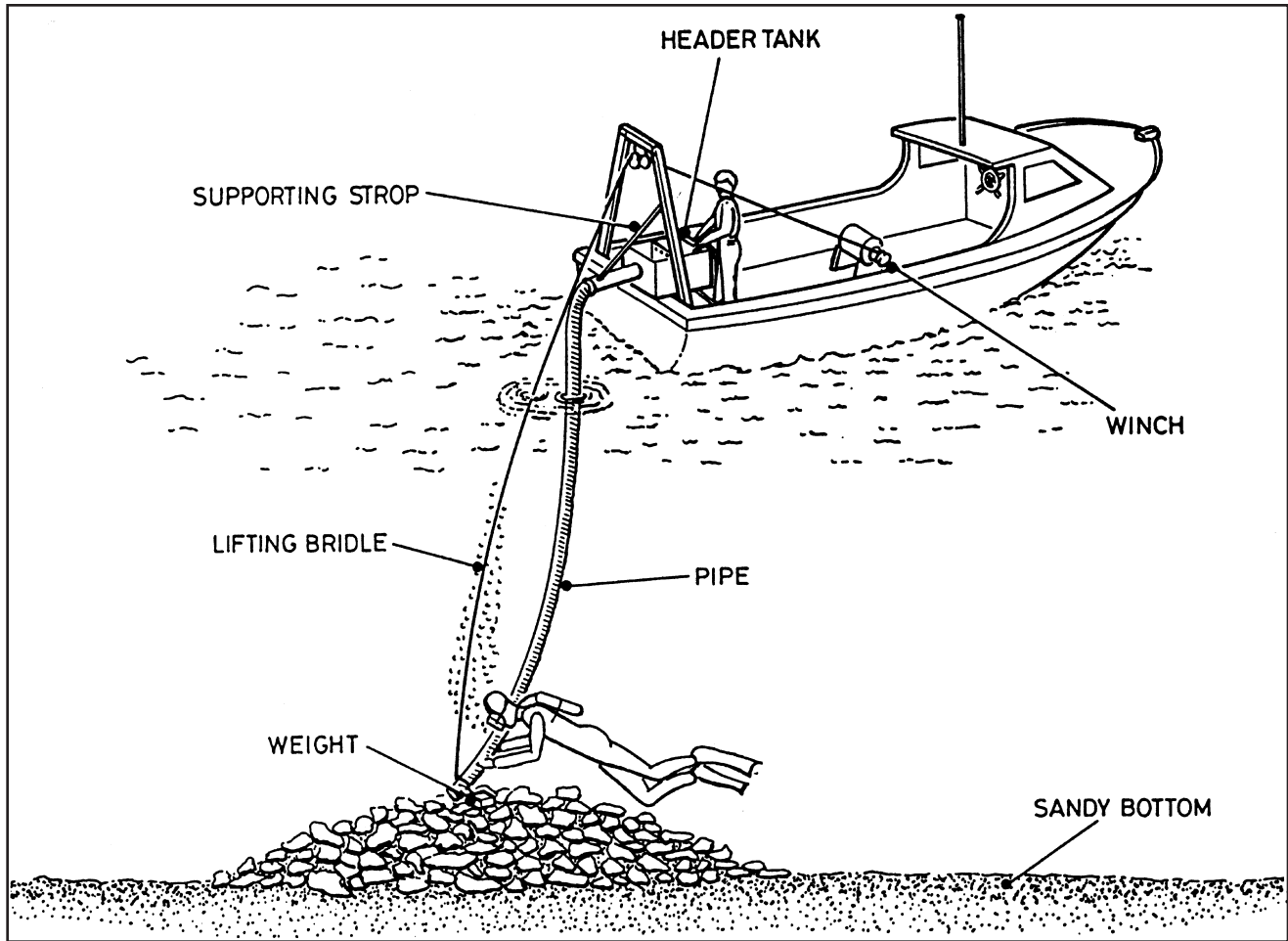


Figure 24.—Diagram of how divers release lobsters via the pipe method. A header tank, incorporating a reservoir is mounted on the stern of the boat and is supplied by a pump. The rear portion of the header tank has a 75 mm diameter fitting to which an armored pump suction hose is attached. The lobsters are gently suctioned through the pipe and directly delivered to the bottom substrate. From Burton (1992). Used with permission.

in the 1950's to less than 30 t in the past few decades (van der Meeren, 1994). The concept of this operation differed from other hatcheries in that *H. gammarus* lobsters were reared under optimal conditions to 1 year of age in a large circular pool (Erenst, 1985; Schjetne, 1987), similar to that described in Van Olst et al. (1977). They are released specifically with the idea of replenishing a depleted stock. The hatchery can produce 120,000 Stage XIII lobsters, but rarely exceeds 30,000–50,000 (van der Meeren¹⁶). Culture techniques

¹⁶ van der Meeren, G. I. Institute of Marine Research, Austevoll Aquaculture Research Station, N-5392, Storebo, Norway. Personal commun. 12 July 1989 and 21 Feb. 1997.

have been described in Erenst (1985) and Grimsen et al. (1987); however, the management of the hatchery has changed and so have the rearing techniques. Since 1989, Norway's Institute of Marine Research has managed this hatchery (van der Meeren and Næss, 1991).

Female lobsters are obtained from the wild for eggs. About 1,000–10,000 larvae are produced from each female, depending upon their size. These larvae are transferred to kreisels (350 l) where they spend 8–18 days, depending on water temperature. Optimal temperature for this growth process is about 24°C which results in Stage IV lobsters in 8–12 days (Uglem¹⁷). During

this time, larvae are fed frozen *Artemia* 2–3 times/day (Grimsen et al., 1987). Mortality is very high during this phase of operation. Under the best of circumstances it is 50%, but more often it is closer to 85% (Uglem¹⁷). Upon reaching Stage IV, the lobsters are transferred to separate boxes as described in Grimsen et al. (1987). Here they are fed frozen *Artemia* 5–7 times/week at 5% of their wet weight. Moist pellets and the computer-controlled feeding system described in Grimsen et al. (1987) are no longer utilized (Uglem¹⁷).

¹⁷ Uglem, I. 1991. Institute of Marine Research, The Lobster Hatchery, P.O. Box 130, 720 Kyrksaeterora, Norway. Personal commun., 22 Nov.

The cost of producing a Stage XIII lobster is estimated at US\$2.00, but with current practices it may now be possible to reduce this cost as much as 30–40% (Uglem¹⁷). From 1979 to 1989, 100,000 1-year-old Stage XIII juveniles were released (Grimsen et al., 1987; Addison and Bannister, 1994) but were not tagged. However, lobsters released into open and/or enclosed areas with artificial shelters and fed blue mussel flesh provided some information on growth and how that affected the density at which lobsters can live. These data suggest a carrying capacity of one 2-year-old lobster/4–5 m², based on releases of 45 1-year-old lobsters into an area of 50 m² and a recapture of 12 lobsters 2 months later, as well as subsequent releases of 36 1-year-olds with a recapture of 11 lobsters after 10 months (Tveite and Grimsen, 1990).

The 715 lobsters retrieved between 1983 and 1988 were distinguishable from wild counterparts by morphological traits (such as double seizer/cutter claws). They ranged in size from <22 cm to >25 cm and included berried females. In 1989, recaptured, hatchery-reared lobsters accounted for more than 50% of the fishermen's catch (Tveite and Grimsen, 1990).

More recently, a pilot-scale experiment at Norway's Austevoll Aquaculture Station involved rearing hatchery lobsters to 1- and 2-year-old juveniles. A total of 9,800 lobsters were marked by branding a spot on either the first joint of the tail or the center of the carapace; these lobsters were then released (van der Meeren and Naess, 1991). These marks are capable of withstanding several molts and are still identifiable once the lobster is recaptured (van der Meeren, 1990). None of these lobsters were recaptured in 1989; however, marked lobsters were recaptured in 1990. These lobsters had increased about 26.5 times in weight and 40% in carapace length (van der Meeren and Naess, 1991).

In 1990, a large-scale release program began using 13,500 1.5-year-old lobsters (21.1 mm CL, 1988 year class) and 7,700 6-month-old lobsters (12.1 mm CL, 1989 year class). These lobsters were tagged with 1 mm binary

coded micro-tags (van der Meeren et al., 1990). This release was the first large-scale release experiment and, from 1991 to 1994, release of 15,000 to 30,000 tagged juvenile lobsters/year occurred (van der Meeren et al., 1990, 1998). Actual releases have been less: 29,693 juveniles were released in 1991, 29,919 in 1992, 17,360 in 1993, and 27,414 in 1994. In October 1992, the first 19 legal-sized male lobsters were recaptured and ranged in size from 83 to 91 mm CL. Their tags revealed that these lobsters were hatched in 1988 and released in April of 1990 (van der Meeren and Naess, 1993), suggesting more rapid growth rates than previously expected. In fact, the cultured lobsters seem to recruit to the fishery within 3–4 years and can support the fishery for at least 5 years. Recapture rates for single year classes range from 5 to 8%. Furthermore, ovigerous females from hatchery origins are now of equal proportion in the population as wild ovigerous females and are thus contributing to the overall reproductive effort in these release sites (van der Meeren¹⁶).

Behavioral traits of hatchery-reared lobsters have also been examined, and they appear to exhibit the same behavior as their wild counterparts. They can adjust their behavior according to shelter and predation risk, light intensity, and individual distance to conspecifics (van der Meeren, 1990). However, van der Meeren (1991a) found that behavioral responses depended on the kind of treatment given to lobsters prior to release. Several stresses were introduced in her study: sudden exposure to light, pressure, and water loss. "Pelagic rushes" (upward swimming) decreased when the number of stresses were reduced. The lowest proportion of rushing and highest proportion of walking appeared in treatments where no stress was applied (van der Meeren, 1991a).

The best transportation methods to release sites were also investigated. First, lobsters were transported to the release site in thermal boxes filled with wet, chilled newspapers and then placed on the bottom directly. However, these animals were very sluggish, slow to gain shelter and, as a result, experienced high mortality (van der Meeren,

1994). Since then, the lobsters have been placed in plastic cages which are then immersed for 30 minutes in a basin of ambient seawater. Observations during release indicated that the lobsters sank slowly to the bottom, landing in a walking position; they then slowly moved into shelters within 20 minutes (van der Meeren, 1991b). Other studies are underway to assess the impact that released lobsters may have on their wild counterparts and to determine population dynamics in the same region without the addition of released lobsters. These studies will provide information to assess whether sea ranching is profitable and whether it represents an effective lobster management tool, particularly in terms of its expense (van der Meeren and Naess, 1993).

France

Prior to 1972, France attempted to build up a reserve of adult lobsters, particularly berried females, by establishing sanctuary zones where all fishing was prohibited. Sixteen zones were established in 1963 and all saw lobster increases (Lorec, 1987; Latrouite and Lorec, 1991). Beginning in 1961, berried females were also stocked in tanks until their larvae hatched, grew, and metamorphosed into Stage VI postlarvae. They were then released into the wild.

Because neither of those techniques produced noticeable improvement in landings, two hatcheries were established in 1972—one on the Isle of Yeu and the other on the Isle of Houat; a third was established later at the Isle of Sein (Lorec, 1987). The hatcheries were designed according to the Japanese system for raising shrimp, rather than the techniques of Hughes et al. (1974). From 1972 to 1977, these hatcheries concentrated on increasing the survival of larvae to Stage V juveniles. They achieved survival rates of 90% to Stage III by feeding larvae to excess on living food, particularly spider crab larvae and *Artemia salina* (which were raised on algal cultures of *Tetraselmis* and *Phaeodactylum*). Survival rates to Stage IV and V were about 75–80% (Audouin, 1974). Up to 250,000 Stage V juveniles were released and 15,000 1-year-old lobsters were released; however, no improve-

ment in landings occurred and it was concluded that these releases were not enhancing stocks (Henocque, 1983; Le Gall et al., 1983).

Beginning in 1978 and continuing through 1983, the hatcheries began to focus on the impact that released Stage V lobsters might have on the fishery. Juvenile lobster marking methods were examined, and hybrids of *Homarus americanus* and *H. gammarus* were used prior to the development of the Bergman-Jefferts microwire tag (Lorec, 1987; Latrouite and Lorec, 1991). Since the only distinctive mark was an extra rostral spine, this method of phenotypically marking released animals was discontinued, but not until after 1,300 1-year-old hybrids were released. Recaptures were expected in 1980 (Audouin, 1981), but none were reported. Fishery statistics were also used to monitor the success of the hatchery efforts, but, as in other countries, natural fluctuations in landings overshadowed any impacts that released lobsters may have made.

Efforts were then directed toward raising 1-year-old lobsters, and in 1984 these 1-year-olds (12 mm CL) were microwire-tagged with 1 mm magnetically coded tags. At the same time, a program was established to determine how juveniles released in natural environments would respond (Latrouite and Lorec, 1991). Juveniles were found to prefer the same types of habitats as postlarval lobsters, particularly algal-covered small rocks with many interstitial spaces between them (Bertran et al., 1985). Optimal densities of juveniles in naturalistic environments were less than 1/m², and the hatchery-reared juveniles were less hardy than their wild counterparts (Latrouite and Lorec, 1991).

Between 1984 and 1987, the hatcheries released 25,480 tagged juveniles directly onto sites believed favorable for their survival. Researchers expected that 4–5 years would elapse before legal-sized lobsters would be recaptured (Lorec, 1987); however, despite low rates of recaptures in 1988 (1 lobster), 1988 (7 lobsters), and 1989 (14 lobsters), nearly all were larger than legal size, indicating a faster growth rate than anticipated (Latrouite and Lorec, 1991). Furthermore, the recaptured lob-

sters remained near or in the site of their release. However, two of the hatcheries were closed before these releases (Lorec, 1987), and, despite the promising initial results, no further juvenile lobster releases were made after 1987 (Lorec, 1987). Since then, restocking efforts and monitoring of recaptures were discontinued since the low number of recaptures was seen as demonstrating that enhancement did not occur (Latrouite, 1998; Latrouite⁴).

Product Enhancement

Product enhancement involves holding low-valued lobsters until they become marketable. Lobsters of lower value may be soft-shelled, missing one or both claws, or one molt away from legal size. Such aquaculture started as early as 1872 in Massachusetts (Anonymous, 1873, 1874) with large quantities (about 40,000) of low-valued lobsters placed into enclosed basins. The lobsters were fed during the summer months only (Anonymous, 1873; Rathbun, 1886). The basins were natural enclosures formed by land or rocks, with one end constructed as a dike (Anonymous, 1873). Results were satisfactory (Anonymous, 1873; Rathbun, 1886), but depended on the influence of the ambient water temperatures.

Because a significant proportion of the Canadian lobster catch is rather small—usually one molt away from legal size (Pringle et al., 1983)—a 5-year Canadian study was undertaken in 1963 to determine the effects of various combinations of temperature, light, lobster density, shelter, diet, sex, size, and maturity on accelerating the growth rates of sublegal lobsters. Females tend to skip molts in order to spawn, so only males were used. Gains in lobster weights were not greater than losses from mortalities and mutilation, and, in most cases, the timing of molting was later than what had been predicted. Consequently, this project was terminated in 1968 (McCleese, 1969). Wilder (1971, 1972) suggested that with the existing state of knowledge, such rearing was not economically feasible. Nonetheless, this kind of culture has been reevaluated several times, because the economic concept is sound, given that the

only other option for selling the sublegal-sized lobsters is to the less lucrative canner business (Aiken and Waddy, 1995).

Eyestalk ablation, which was first recognized to accelerate molting and growth by Zeleny (1905), was fully investigated. Mechanisms controlling molting were studied and reviewed by Passano (1960) with such information creating a baseline for experiments with ablated lobsters. Initial work, however, produced conflicting results. Flint (1972) reported that bilateral eyestalk ablation on American lobsters increased, rather than decreased, the time between molts. In contrast, others succeeded in accelerating the molt cycle with ablated lobsters but at the cost of lower survival (Rao et al., 1973; Sochasky et al., 1973). Stewart and Castell (1976) suggested that poor survival in ablated lobsters was related to diet and nutrition, as was observed in crayfish by Smith (1940).

Further experiments demonstrated that eyestalk-ablated lobsters fed an adequate and balanced diet were capable of increased growth and high survival (Mauviot and Castell, 1976; Bishop and Castell, 1978); consistent weight gains of 70% were achieved (Bishop and Castell, 1978). More recently, Coulombe and Motnikar (1989) experimented with two methods of unilateral eyestalk ablation: removal by excision and cauterization and removal by strangulation. Lobsters 76–81 mm CL were kept in an open seawater system with ambient water temperatures and natural photoperiods. All lobsters were fed to satiation with thawed herring and shrimp. However, neither of these two methods had a significant effect on the molt rate (Coulombe and Motnikar, 1989).

Owing to the variable eyestalk ablation results, cage culture methods were reassessed, and in 1983 a suspended floating system yielded encouraging results (Fradette, 1984a, b; Fradette et al., 1987). Lobsters ranging from 76 to 90 mm CL were maintained on crab, *Cancer irroratus*, or pelleted diets described in Gagnon et al. (1984). Cost studies, with respect to time, personnel, and marketing needs yielded the first economic feasibility study for a firm

engaged in semi-intensive lobster cultivation (Fradette et al., 1987).

More recently in the Bay of Fundy, Young-Lai and Aiken (1989) grew sub-legal (75.2 to 80.9 mm CL) lobsters in cages through one molt to commercial size. These lobsters were fed on a diet of commercial salmon ration and raw herring, and the biological feasibility of culturing lobsters in cages through one molt was demonstrated. However, there were no data on the venture's economic feasibility.

In Scotland, a different approach was used by Futch beginning in 1968 (Munday, 1969). Immature or marketable lobsters were placed in "cages" (12 m wide \times 12 m long \times 2.4 m deep), which were anchored in sheltered coves at sufficient depths to avoid freshwater runoff from the shore. Lobsters were maintained on "trash" fish (from local fishermen) and crabs, but they also fed on organisms growing on the cage material. These lobsters were held until the market price was high or until immature lobsters grew to marketable size (Munday, 1969; Bowbeer, 1971). Despite its success (Bowbeer, 1971), operations ceased shortly after 1971, due to a disagreement between landowners (Burton¹⁸).

Full Grow-out

Interest in culturing lobsters from egg to maturity arose in 1900 at Wickford, R.I. (Mead, 1902; Mead and Williams, 1903). After hatching and rearing larvae to Stage IV, the lobsters were placed communally into "cars." These cars were constructed with galvanized iron screen sides which permitted free circulation of water. Each car was provided with sand, gravel, seaweed, etc., to simulate natural habitats. During the summer months, these cars were suspended from a floating houseboat to a depth of 45 cm. The lobsters were maintained at ambient seawater temperatures and fed various foods. In the fall, the cars were lowered to about 2.4–3 m deep and maintained there until spring. During the winter months, lobsters were

not fed; however, food may have been obtained from particles in the water or from animals growing inside the cars such as mussels, oysters, and marine worms.

The first growing season produced encouraging results with lobsters ranging in size from 106 to 159 mm TL, with a mean of 122 mm. While these experiments were exploratory and inconclusive, they did demonstrate great variability in growth rates between communally reared lobsters, with the greatest growth rates occurring in those lobsters reared at lower densities (Mead, 1902; Mead and Williams, 1903). This variation in growth rate has been confirmed by more recent researchers in California and Canada (reviewed by Van Olst and Carlberg, 1979; Waddy, 1988; D'Abramo and Conklin, 1985).

Growth data from earlier studies at Wickford also provided some insight on estimating lobsters' growth rate in nature (Hadley, 1906a). John Hughes at the Massachusetts State Lobster Hatchery retained individual Stage IV lobsters from each year's hatch to study growth rates and held some animals for as long as 10 years (Hughes and Matthiessen, 1962, 1967). Lobsters were maintained at ambient seawater temperatures and fed on fresh fish and shellfish. Records were kept on molting frequencies, growth rates, food requirements, and mating behavior (Hughes and Matthiessen, 1962, 1967). These lobsters were hatched and reared to legal size (about 450 g) in a little over 3 years, as opposed to the 6–10 years required in nature.

Given these advantages, Hughes speculated that commercial lobster farming was possible (Hughes, 1968b). By rearing lobsters in optimal levels of salinity and oxygen, providing them with proper food, and keeping the temperature at a constant 20°C, market-sized lobsters could be produced in less than 2 years (Hughes et al., 1972). A further reduction in this time was obtained by phenotypic selection of fast growing lobsters (Hughes et al., 1972), and owing to these successes, several experimental lobster farms arose (Shleser, 1971; Shleser and Tchobanoglous, 1974; Van Olst and Carlberg, 1979).

Communal rearing systems were also designed which were less complex, less expensive, and required less space. Although these rearing systems experienced some success, low survival and nonuniform-sized lobsters were major flaws (Van Olst et al., 1976a; Sastry and Zeitlin-Hale, 1977; Carlberg et al., 1979). These problems were partially alleviated by providing a variety of substrates in the communal tanks (e.g. oyster shells), as well as by sorting out individuals according to their size and removing their chelipeds (Aiken and Young-Lai, 1981; Aiken and Waddy, 1988; Waddy, 1988; Waddy et al., 1988).

Likewise, many experimental systems have been developed and analyzed for the complete grow-out phase from juvenile to market size (Schuur et al., 1974; Sastry, 1975; Hand et al., 1977; Van Olst et al., 1977; Mickelsen et al., 1978; Richards and Wickins, 1979; Conklin et al., 1981; Beard et al., 1985; Ingram, 1985). Of these newer systems, the flushing tray designed by researchers at the St. Andrew's Biological Station, Can., and the University of California, San Diego, appeared to yield the best results (Van Olst et al., 1976b). Other advancements have been made with automatic feeding systems developed for larval (Serfling et al., 1974b; Fig. 13) and juvenile rearing (Grimsen et al., 1987; Wickins et al., 1987). Several systems have also been developed to rear juvenile lobsters individually (Chanley and Terry, 1974; Lang, 1975; Conklin et al., 1981; Beard and Wickins, 1992; Burton, 1992). A complete description of these culturing techniques can be found in Aiken and Waddy (1995).

Experimental pilot-scale operations for commercial lobster production were attempted by some in the 1970's, utilizing much of the knowledge gained from work by Hughes (1968b), Hughes and Matthiessen (1962, 1967) and from the communal rearing studies of Van Olst et al. (1976a), Sastry and Zeitlin-Hale (1977), and Carlberg et al. (1979). Unfortunately, economic reasons and lack of biological information brought an end to these projects. For example, in the mid-to-late 1970's, a "mini" lobster farm was created at

¹⁸ Burton, C. A. 1991. Sea Fish Industry Authority, Marine Farming Unit, Ardtoe, Acharacle, Argyll PH36 4LD Scotland. Personal commun., 24 Apr.

the Long Island Lighting Company's power generating station in Northport, N.Y. Together, Frederick B. Wishner of New York, Anthony D'Agostino from the Marine Science Institute at Montauk, N.Y., and Christopher Gross, a biologist from Long Island Lighting Company in Hicksville, N.Y., successfully reared lobsters in cooling waters from the power generating station in a canal (Portersfield, 1982). Unfortunately, this culture effort lasted only about 6 months (Gross¹⁹). Another attempt was made by A. Gmeiner in Woodside, N.Y., in the early 1970's using a closed water system in the basement of his home. However, his lobsters contracted a disease, caused by *Fusarium* sp., which resulted in heavy mortality prior to molting (Lightner and Fontaine, 1975), and this farm was also discontinued (Fontaine²⁰).

These early failures did not discourage further experimental studies, but the lobster was fully assessed to determine if it met such essential requirements for commercial aquaculture as consumer demand, profit potential, ability to reproduce in captivity, simple larval development, high food conversion efficiency, and resistance to disease (Gates et al., 1974; Cobb, 1976). Because it did meet several of the requirements, it was selected by the National Oceanographic and Atmospheric Administration as one of the four marine animals having a "high priority" for aquaculture (Glude, 1977; Van Olst and Carlberg, 1979; Van Olst et al., 1980). The major U.S. researchers involved in such research were based at San Diego State University, Bodega Bay Marine Laboratory, the University of California at Davis, Woods Hole Oceanographic Institution, the University of Rhode Island, the University of Maine, and the Massachusetts State Lobster Hatchery (Van Olst and Carlberg, 1979). Private-sector research was also conducted by Sanders Associates of New Hampshire

and Aquaculture Enterprises of California (Hall, 1979; Anonymous, 1987a). Similarly, the Department of Fisheries and Oceans in Canada also supported such research (Ford and Van Olst, 1975; Van Olst et al., 1980; D'Abramo and Conklin, 1985), and the United Kingdom promoted programs culturing the European lobster, *H. gammarus*, to marketable size (Richards and Wickins, 1979; Anonymous, 1980; Richards, 1981; Beard et al., 1985).

Nutritional requirements were also examined to help formulate diets for cost-effective growth. Diets composed of material that lobster larvae would never encounter in nature have been extensively examined. These include feeds such as living *Artemia* cysts or adults (Conklin et al., 1975; Carlberg and Van Olst, 1976; Conklin et al., 1978; Rosemark, 1978; Capuzzo and Lancaster, 1979; Bordner et al., 1986; MacKenzie, 1987), frozen adult brine shrimp (Hughes, 1968b; Rosemark, 1978; Good et al., 1982; Eagles et al., 1984, 1986), ground beef and beef liver (Herrick, 1895; Emmel, 1908), shredded or crushed fish and crab tissues (Herrick, 1895; Emmel, 1908; Smith, 1933 with *H. gammarus*; Templeman, 1936), chopped soft-shelled clam (Mead and Williams, 1903; Barnes, 1906a), or artificially prepared foods (Castell and Budson, 1974; Conklin et al., 1975, 1977, 1978; Rosemark, 1978; Capuzzo and Lancaster, 1979; Bowser and Rosemark, 1981; D'Abramo et al., 1981; Bordner et al., 1986).

Purified diets—HFX CRD 84 consisting of crab protein concentrate, wheat gluten, corn starch, celufil, cod liver oil, corn oil, minerals, and vitamins (Boghen et al., 1982) or BML 81S consisting of casein, egg white, wheat gluten, corn starch, celufil, cod liver oil, corn oil, soy lecithin, minerals and vitamins (Conklin et al., 1980)—show good growth and high survival, while pelleted diets have had variable success. However, pelleted diets incorporating natural food items, such as mysid shrimp, crab, and crangon shrimp have shown some promising results (Cook and Worsley, 1986). In contrast, *Artemia* flake formula does not seem to promote high survivability, but it may be

useful as a supplement (Burton, 1991, 1992). Further studies are underway to develop a better pelleted diet (Burton, 1992). These studies have mainly served to show the superiority of one type of diet over another in terms of cost, survival, and larval growth.

The studies on artificial diets, in particular, have shown that long-chain polyunsaturated fatty acids are extremely important for the survival of both the larvae and postlarvae. Because of its low cost and ease of use, *Artemia salina* is an excellent food source for rearing larvae from hatching through the first 6 months of growth (Aiken and Waddy, 1989); however, different types of brine shrimp vary in fatty acid content and thus in quality (Fujita et al., 1980). While optimal feeding schedules for live and frozen *A. salina* have been determined (Carlberg and Van Olst, 1976; Aiken and Waddy, 1989), the lack of development of a cost-effective, adequate diet continues to be a major hindrance to commercial lobster culture today (Waddy, 1988). Recent and extensive bibliographies on crustacean nutrition (Castell and Boston, 1990; Conklin, 1995) will be of great assistance to those interested in developing artificial diets.

Broodstock management techniques have been developed using preovigerous wild female lobsters (Waddy and Aiken, 1984a). By using the indices of Perkins (1972) and Hepper and Gough (1978) for embryonic developmental rates, researchers have been able to calculate and control the time of hatching for *H. americanus* and *H. gammaurus*, respectively (Schuur et al., 1976; Richards and Wickins, 1979; Beard et al., 1985; Beard and Wickins, 1992; Burton, 1992). Furthermore, year-round production schedules for eggs (Waddy and Aiken, 1992) and larvae (Waddy and Aiken, 1984a, b; Aiken and Waddy, 1985) are now available.

Private-sector research has also provided useful information for aquaculture. In 1974, when an ex-lobsterman, Emile Plante (Chapman¹⁴), with a novel patented initial habitat design approached Sanders Associates of New Hampshire, the company elected to initiate a research and developmental program to

¹⁹ Gross, C. 1991. Long Island Lighting Company, 175 East Old Country Road, Hicksville, NY 11801. Personal commun., 6 Dec.

²⁰ Fontaine, C. T. 1991. National Marine Fisheries Service, NOAA, Galveston Laboratory, 4700 Avenue U, Galveston, TX 77550. Personal commun., 6 Dec.

explore the feasibility of lobster culture (Anonymous, 1979). Lobsters were reared for 5 years at Kittery, Maine, at accelerated temperatures on special diets (Hall, 1979). A similar, 2-year program was conducted in Nashua, N.H. (Chapman, 1983; Chapman et al., 1988) to confirm experimental assumptions and concepts, develop prototype equipment, and show the viability of commercial lobster production (Hall, 1979). Those experimental and pilot programs helped develop a licensable technology package for the American lobster culture (Chapman et al., 1988).

Unfortunately, commercial production did not proceed for several reasons, including, but not limited to, high oil prices (which affect construction costs of the equipment made of plastic), increased wild lobster landings (Anonymous, 1979), the absence of an artificial diet, and the expense to heat seawater to optimal levels (Fig. 25). Nonetheless, several hundred lobsters were raised to marketable size (Chapman¹⁴). Methods to conserve these costs were investigated in the United States and Europe in the form of recirculating culture systems (Hand et al., 1977), solar powered systems (Portersfield, 1982), and the use of cooling waters from electric

power generating stations, as originally recommended by Dow (1969), Klopfenstein and Klopfenstein (1974), and Shleser and Schuur (1975).

Researchers found that market-sized lobsters originally raised from eggs could be grown in 2 years by using thermal effluent (Van Olst, 1975; Ford et al, 1976; Van Olst et al., 1976b; Van Olst and Carlberg, 1978). However, concerns arose about toxic chemicals being present in this type of water. Becker and Thatcher (1973) described a large number of elements and chemicals (e.g. copper, zinc, cadmium, cobalt, chlorine, chromium, lead, arsenic, and acids) found in effluents and their possible effects on aquatic life, particularly those on growth and fecundity (Bowen, 1966; Sprague, 1969). Both compounds and temperature regimes associated with thermal effluent were examined using various life history stages of the lobster (Dorband, 1975; Dorband et al., 1976; Ford et al., 1976, 1979; Johnson, 1977; Felix, 1978) and were found to be nontoxic and unimportant in lobster culture. Pilot facilities were then proposed and evaluated for the commercial culture of lobsters with effluent water (Wright, 1976; Turner et al., 1979). Despite these pilot studies,

commercial production was still considered economically unjustifiable.

Nevertheless, because of the potentials involved, mathematical models of lobster culture facilities were developed (Rauch et al., 1975; Botsford, 1977). These models have been used to project culture costs, determine accuracy of projections through sensitivity analysis, and to determine optimal culture methods (e.g. temperature, container size, and flow rates) (Johnston, 1976; Botsford et al., 1977, 1978; Johnston and Botsford, 1980). Costs of space, land, buildings, tanks, structure, and trays (Allen and Johnston, 1976), as well as waste treatment costs based on flow rates (Tchobanoglous and Shleser, 1974), were assessed using thermal effluent for aquaculture (Fig. 25) and culminated in a book on the subject (Allen et al., 1984).

Others have studied the feasibility of producing 1,000,000 1-pound lobsters annually, with a general description of a computerized facility (Coffelt and Wickman-Coffelt, 1985). Their projections include capital costs in excess of \$31 million with an annual operating cost of over \$3 million. Thus, pilot-scale projects were suggested and started up in Provo, Utah (more than 800 miles from the ocean), on the remote Caribbean Island of Anguilla, in California, and in Hawaii.

In Provo, Utah, two Brigham Young University graduate students, Rex Infranger and Roger Mickelsen, developed a program involving the use of artificial seawater, solar power, and a system of cages (Mickelsen et al., 1978). They reported successfully raising 1-pound lobsters in 21–30 months by using special diets and temperatures of 22°C (Portersfield, 1982). A brief description of their experimental lobster farm and their claim of producing 1,000,000 lobsters a year is presented in Hemming (1981). Currently, an upgraded cage system designed and built based on the original version exists (Mickelsen et al., 1978), but, due to the proprietary nature of this project, information has been limited. However, they operate a functional pilot plant facility with everything from hatching to grow-out capability with expectations of mar-

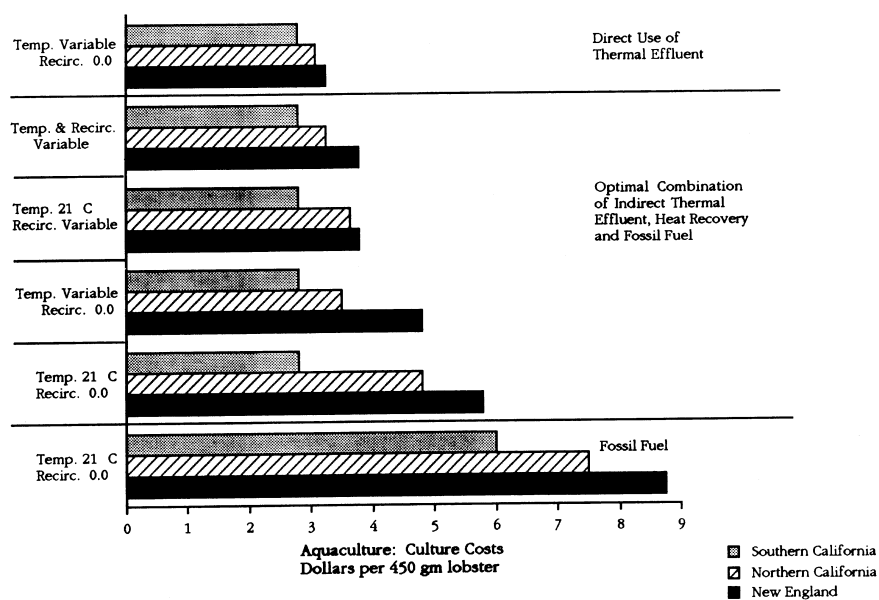


Figure 25.—Culture costs using three sources of fuel: fossil fuel, thermal effluent and fossil fuel, thermal effluent. (Adapted from Botsford et al., 1978).

keting their product in the near future (Infranger²¹).

The commercial lobster farm on Anguilla, West Indies, applied culture techniques similar to those of the University of California and the Massachusetts State Lobster Hatchery, and their accomplishments are reviewed in Belleville (1981).

Aquaculture Enterprises (AE) spent 12 years in California experimenting with lobster domestication. Most of their technical support came from the Sea Grant College Programs of the University of California, Davis, the Bodega Bay Laboratory, the University of Maine, and from St. Andrew's Biological Station in New Brunswick, Can., (Loupe, 1991). AE has taken the concept of "lobster farming" from a biological potential to a demonstrated, economic reality. The AE cost-efficient growing system produces cultured 1-pound lobsters which are price- and taste-competitive with wild lobsters. Domestication involved a multidisciplinary approach involving water chemistry, physiology, pathology, nutrition, systems engineering, and reproduction (Wilson, 1980). AE's husbandry and bioengineered technology, combined with the discharged sea water from southern California's Edison Coastal Power Plant, resulted in a 3-year marketable lobster, a 70% survival rate, a reproduction rate 60% that of wild lobsters, and a food conversion ratio of 4.5:1—all for less than \$3.50 a pound production cost (in 1986 prices) (Anonymous, 1987a).

In 1988 AE relocated to Hawaii where they now raise lobsters by mixing the warm surface waters off Hawaii with the deep colder waters, thereby achieving a 22°C temperature in which the lobsters thrive. AE has also developed special husbandry techniques incorporating a plastic grid of their own design (Anonymous, 1990) and their own feeding techniques using local fishing waste (Loupe, 1991). In 1990, AE had some 5,000 animals in residence (Anonymous, 1990). Currently, AE is working on broodstock strains, testing feeding rations, and experimenting with prototype production equipment (Wilson²²).

Kona Cold Lobster, Ltd. in Hawaii is currently farming a unique blue lobster. By mating the *H. americanus* with an *H. gammarus*, the result is a hybrid lobster that is bright blue in color. Their product is being marketed to the aquarium trade and as a garnish for seafood platters in up-scale restaurants (HAAC, 1996).

Transplantation Programs

Homarid lobsters are generally limited in distribution to the north Atlantic Ocean. *Homarus americanus* inhabits the northwest Atlantic coast from North Carolina to Labrador, while *H. gammarus* inhabits the northeast Atlantic coast from Norway to Morocco (Cooper and Uzman, 1980). Prior to heavy commercial exploitation, *H. gammarus* also occurred in parts of the western Mediterranean (Williams, 1988; Holthius, 1991). Because of these cold-water limitations, transplantation programs beginning in the late 19th century were attempted as a way to increase yields from the lobster fishery. This involved transplanting homarid lobsters to the Pacific Ocean, where suitable environmental conditions exist (Van Olst et al., 1980). Such efforts date to 1873 and to 1889 for the States of California and Washington, respectively (Rathbun, 1892). Nothing resulted from those early attempts, but there are a number of historical reviews on the attempts that followed (Perrin, 1876; Stone, 1882; Ryder, 1886a; Smith, 1896), including a full account compiled by Rathbun (1890). In Canada, transplantation of lobsters to the east coast of Vancouver Island, B.C., was attempted first in 1896 and again in 1905 and 1908 (Fraser, 1916). However, since there was no controlled observation of these animals after transplantation, no information is available on the fate of these lobsters. These transplantations are reviewed by Butler (1964).

In 1965, several thousand Stage I and Stage IV larvae were experimentally transplanted from the Massachusetts State Lobster Hatchery (Anonymous,

1966) to Fatty Basin on the west coast of Vancouver Island. This was followed by the introduction of an additional 5,000 adults between 1965 and 1966 (Ghelardi, 1967). Meanwhile, construction began in 1967 to establish a hatchery at Fatty Basin, and by May, 123 large "berried" females for broodstock were air-shipped from George's Bank (Ghelardi and Shoop, 1972). These transplantations demonstrated that lobsters would grow, survive, reproduce, and behave normally in Pacific waters (Ghelardi and Shoop, 1968, 1972). Barber (1983) reviewed these earlier experiments and concluded that, with the present knowledge of the physical parameters (temperature, dissolved oxygen, etc.) of the Masset system, transplanting of lobsters to Masset Inlet may be feasible.

During the early 1970's, California once again attempted to develop an American lobster fishery along its coast (Ford and Schuman, 1971; Ford and Krekorian, 1972, 1973). However, due to the competitive interactions between *H. americanus* and *Panulirus interruptus*, which showed that *H. americanus* would displace *P. interruptus*, release of wild American lobsters was not recommended (Krekorian et al., 1974; Lester, 1975).

More recently, Canadian workers transplanted 2,174 males (81–114 mm CL) and 2,310 nonovigerous females (81–112 mm CL) to St. Michaels Bay in Labrador (Boothroyd and Ennis, 1992). While these lobsters were capable of molting, mating, and reproducing, most of the female lobsters resorbed their eggs, and those few that did extrude were not capable of generating and supporting a fishery.

Japan also tried to introduce American lobsters into its waters as early as 1915. Those earlier introductions were not successful, but Jiro Kittaka more recently attempted to transplant both *H. americanus* and *H. gammarus* (Kittaka, 1980; Kittaka et al., 1983). Initial experiments began with egg-bearing females of both species from the Massachusetts State Lobster Hatchery, the Centre Oceanologique de Bretagne and Association Peche Aquaculture Sud Bretagne in France, and the University College in Galway, Ireland (Kittaka, 1990). Larval rearing was first attempted with the

²¹ Infranger, R. 1992. Sea Inc., 560 South 100 West, Provo, Utah. Personal commun., 10 May.

²² Wilson, P. L., III. 1990. Aquaculture Enterprises, P.O. Box 3314, Kailua-Kona, HI 96745. Personal commun., 26 Nov.

planktonkreisel, but later an outdoor octagonal tank (1.8 m deep) was used (Kittaka, 1980, 1990). Stage IV *H. americanus* lobsters were released at Koshiki Islands near Kyuski in 1981. This was followed by another release in 1982 of 156 Stage IV and V lobsters and 97 Stage XI–XV lobsters. These experiments were carried out on artificial reefs (cement blocks) and in cages (3 m wide × 3 m long × 0.3 m high) designed for monitoring (Kittaka et al., 1983).

Observations revealed that both size groups exhibited burrowing behavior similar to conspecifics in the Atlantic (Kittaka et al., 1983). All *H. americanus* lobsters dispersed from the release site, but 30% of *H. gammarus* lobsters remained under their shelters. Furthermore, both species successfully reproduced in cages and in large pools (Kittaka, 1984a). Grow-out was conducted in outdoor tanks covered with a 10 cm layer of oyster shells on the bottom (Kittaka, 1984a). Lobsters were fed natural foods with supplements of crushed mussels and/or shrimp pellets (Kittaka, 1988) and held communally at densities of 5–710, with a survival rate estimated at 82–89% (Kittaka, 1984a).

Homarus gammarus grew faster than *H. americanus* up to Stage XVII, but *H. gammarus* was smaller in body weight after Stage XII and in total length after Stage XVIII (Kittaka, 1984a). Reproductive size, 540 g, was attained in 4–5 years (Kittaka, 1984b) and these lobster species are currently breeding in the local waters of Sanriku. Because of the slower growth rates of the European lobster, it is believed that the American lobster will be a more suitable candidate for mass introduction (Kittaka, 1988). Furthermore, *H. americanus* is expected to pose no threat to Japanese littoral organisms, but they may affect the native shrimp (Kittaka, 1988).

Soft-shelled Product

The concept of aquaculture is not new and it is believed by Wear (1990) that methods like those which produce soft-shelled crabs may be applied to the lobster. In the late 1800's, soft-shelled lobsters were said to be an excellent food (Mather, 1894). Recently, it has been suggested that just as soft-shelled

crabs and crayfish have become a gourmet food in many restaurants, the lobster too can be marketed in this way (Wear, 1990). Research and development is needed to determine market demand, system design, control of molting, and pilot operations, which could eventually lead to commercial viability. Furthermore, if lobsters are accepted as a soft-shelled product, the possibility of marketing them at smaller sizes similar to that of the crayfish exists (Wear, 1990). Also, if a market is established for a legal-sized, soft-shelled product, an outlet would then be open for lobstermen to sell their soft-shelled catch during molting season.

Conclusions

Although economics will decide the eventual fate of lobster hatcheries and stock enhancement programs, much biological information has already been gained from them. While some hatcheries still haphazardly release postlarvae into coastal waters without regard for possible impacts on naturally recruiting postlarvae (such as displacement), others are currently providing important information on the survival of recent benthic recruits and how long they take to enter the fishery. Such information will not only be useful in predicting year-to-year fluctuations in landings, via management models, but also will provide better assessments of the value of "seeding" waters with postlarvae and/or juvenile lobsters. Acquisition of these data, as well as the supplying of stock for biological experiments, requires the operation of a hatchery in any district, state, or country where a commercially important fishery exists. Although hatcheries should not be used to replace current management strategies for fishable wild stocks, they can be used as a stock enhancement research tool, wherever deemed necessary for the health of the fishery.

However, any stock enhancement must be conducted in a responsible manner which will provide the best possible outcome for the survival of stocked and wild lobsters. This may mean employing and stocking artificial reefs in areas currently unsuitable for new benthic recruits, as well as determining the effect that hatchery-stocked

animals have upon naturally recruiting populations.

Great Britain, Norway, and Scotland have demonstrated that hatchery-reared lobsters do survive after release, are capable of reproduction, and can enhance existing wild populations. In fact, if hatchery-reared juveniles are released onto carefully selected substrates, they are capable of adding to the commercial stock within 4 to 6 years following release.

These results are encouraging and should result in the reassessment of how hatcheries can be used in the future—particularly as hatchery functions have shifted from mostly research-oriented practices to mostly stock-enhancement practices. For the future we hope that hatcheries will again pursue rigorous research programs in addition to their stock enhancements programs, as they have a proven research track record and great potential for further investigations.

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