

A Simulation Study of Sex Ratios and Regulation Effects with the American Lobster, *Homarus americanus*

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Abstract

Computation of a surplus production curve for the Rhode Island lobster stock provided some indication of an association between low parental stock density and low surplus production. A model of lobster stock composition was constructed to permit examination of stock composition under varying conditions of simulated exploitation, natural mortality, and regulation. The theoretical effects on sex ratios of the decreased molt frequency of mature females as well as regulations for protecting berried females and the double-gauge regulation were examined. The results of these model studies suggested that the double-gauge regulation which involves protection of large animals has no biological significance due to the small numbers remaining in the population under the conditions studied. On the other hand, protection of berried females clearly produced higher proportions of females in the stock. In addition, the average fecundity of model lobster stocks with protection of berried females was consistently higher than with no protection.

THE ECONOMIC IMPORTANCE of the fishery for the northern lobster, *Homarus americanus*, is steadily increasing in the New England states and the Canadian maritime provinces. In addition, significant changes are taking place in portions of the fishery. An illustration of this change is shown in the recent lobster landings for Rhode Island (Fig. 1). From this figure there is some suggestion of a fairly stable inshore pot fishery, but the trend in landings of offshore (trawl) lobsters demonstrates a significant increase in recent years. This trend is also reflected elsewhere in New England. The relatively recent advent of the offshore trawl fishery has prompted further investigations of various aspects of lobster life history. Much of the current work in the United States is being coordinated by the U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, West Boothbay Harbor, Maine. Prior to and during the acquisition of new data it also seems highly desirable to attempt a synthesis of available information in order to better assess our present position, and to point out important gaps in our knowledge.

Prior to the turn of the century lobster regulations, which include protection of berried females, have been in effect in the United States and Canada. More recently, regulations protecting berried female European lobsters have been introduced in Europe. The state of Maine has also imposed a so-called double-gauge regulation which prohibits the taking of all lobsters beyond a designated maximum length (carapace length of 5 inches). The double-gauge regulation has recently been considered for adoption by Massachusetts. In spite of widespread adoption of regulations protecting berried females, some skepticism concerning their value has been expressed by Wilder (1965). In view of the obvious practical difficulties in enforcing any marine fishery regulations,

they should be clearly justified on biological and/or economic grounds or otherwise eliminated.

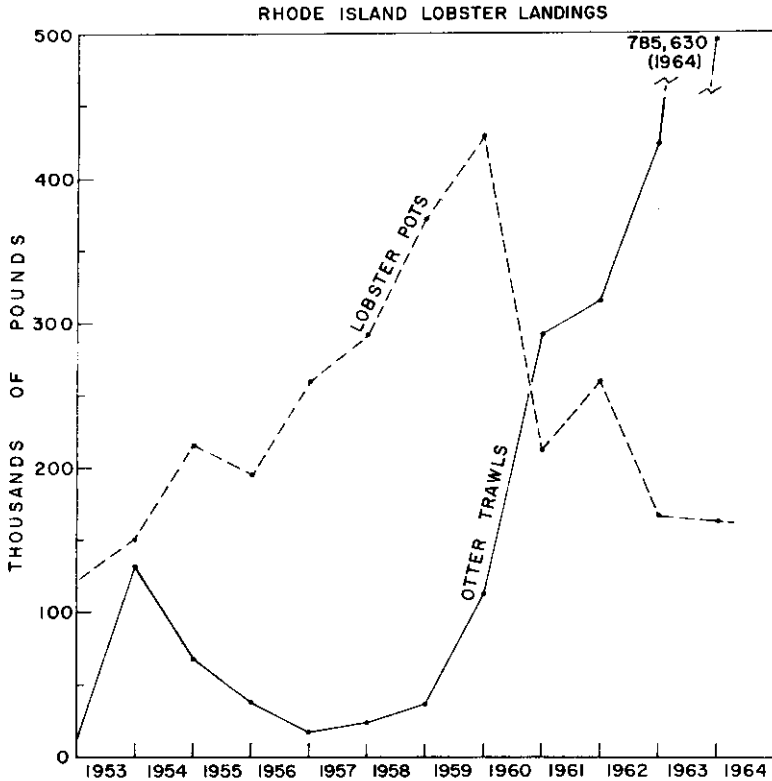


FIG. 1. Rhode Island lobster landings for the period 1953-1964

This report considers available empirical data and a theoretical model of a lobster population in an effort to assess the value of regulations with respect to the protection of berried females and larger female lobsters. The theoretical model is based on available empirical data concerning growth, maturity, fecundity, and molt frequency using a range of values for natural and fishing mortality coefficients combined with simulated protection and no protection of berried females. It is suggested that the unique life history characteristics of the female lobster (particularly reduced molt frequency and consequently reduced growth of mature females as well as unique mating behavior) warrant further appraisal of regulations dealing with their protection.

STOCK AND RECRUITMENT

Before proceeding with the lobster stock composition model it is desirable to attempt a further examination of the relationship between lobster stock and

recruitment. Efforts have been made to assess the reproduction of Canadian lobster stocks by means of larval surveys (Scarratt, 1964), but no conclusive relationship was demonstrated between the larvae and subsequent stock. Wilder (1965) concluded from studies also made in Canada that it seems unlikely that abundance of egg-bearing females is an important factor in limiting commercial production.

Several attempts have been made to relate stock density to yield directly in the case of marine fishes (Graham, 1935; Schaefer, 1954; Ricker, 1958). The latter method involves the postulate that the greatest harvestable surplus is obtained at some intermediate level of abundance, and that lowered surplus production occurs at higher or lower stock densities. Such a density dependence was also suggested by Scarratt (1964) in attempting to explain some aberrant data. To obtain another indication of the relationship between stock density and surplus production, Rhode Island data on catch and effort from the inshore fishery for a 22 year period were analyzed (Fig. 2). An asymmetrical surplus production curve was fitted to a plot of surplus production versus stock density five years previously. A five year lag was used because the laboratory growth data of Hughes and Matthiessen (1962) and Rhode Island data of Hadley (1906) suggest a catchable size (approximately 80 mm carapace length) may be achieved in this period. It also appears that the new recruits contribute substantially to the fishery during their first year inasmuch as exploitation in the lobster fishery is generally high. Details of the computations of surplus production for the Rhode Island lobster stock are provided in Appendix 1 and Table 4. The method used follows that described by Ricker (1958), Example 12E, p. 260. The data points of Fig. 2 are widely scattered and provide little indication of the true form of the surplus production curve. However, the frequency of points below and to the left of the dome of the curve suggests that there may be some tendency for the years with the smallest stock to have the smallest surplus production five years later. Obviously, this statement is dependent on the validity of the position of maximum equilibrium yield. The wide scatter of points also suggests an important effect of environmental variables on recruitment.

MODEL DEFINITION

The assumptions and model parameters utilized herein are approximately the same as those described by Thomas (1955). However, the nature of the model is quite different because protection of berried females is incorporated, and therefore the model will be described in detail. In accordance with Thomas (1955) it is assumed that recruitment is uniform with a fifty-fifty sex ratio at the onset of maturity. It is further assumed that mature male lobsters molt annually and that mature females molt every other year in alternation with the berried condition. The berried condition is assumed to last for 12 months. For purposes of converting time to length, a uniform total length increase of 14 percent is utilized. Although sizes at maturity of 9 and 11 inches (total length) were utilized for some of the computations, the inferences made from model data are not strictly dependent on absolute size at maturity nor upon a uniform molt frequency, which was also assumed for simplicity.

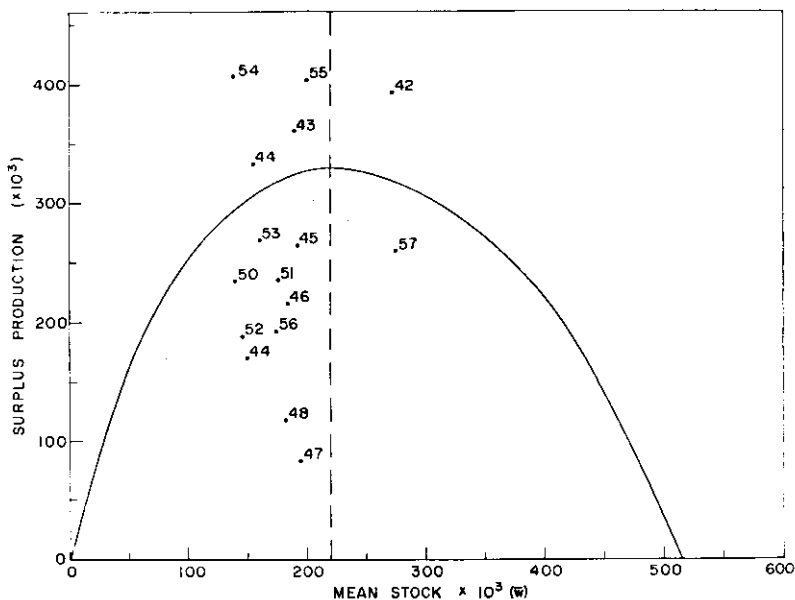


FIG. 2. Surplus production (equilibrium catch) of inshore lobsters in Rhode Island plotted against stock density 5 years previously, with an asymmetrical surplus production curve fitted by the method described in Appendix 1.

Specifically, the exponential (logarithmic) model of the decrease of 1,000 male and 1,000 female lobsters was examined over a 10 year period for a range of total mortality coefficients from 30-80 percent. Survival of the male lobsters is given by:

$$N_{t_L} = N_0 e^{-Zt_L}, \quad j = 0, 1, 2, \dots \quad (1)$$

$$j + 1 \geq t_L \geq j$$

Protection of berried females was incorporated into the model in the following way: Relate the time intervals to size (t_L) by assuming a uniform length increase per molt. That is t_L may be defined as a length dependent time scale, with a constant expressing the percentage increase in total dimension per molt. Since the females are non-berried in the first year and berried in the second without a change in size we have two sets of values for the females over t_L — one for the berried and one for non-berried specimens. This provides two sectionally continuous curves over the length dependent time interval t_L which are related to survival. In the case of males one continuous curve (an exponential decrease) relates t_L to survival as shown in equation (1). It follows that by protecting females in the berried condition their rate of decline over t_L will be less than in the non-berried state.

In the non-berried state survival of females over t_L is given by:

$$N_{t_L} = N_j e^{-Z(t_L - j)}, \quad \begin{array}{l} j = 0, 2, 4, \dots \\ j + 1 \geq t_L > j \end{array} \quad (2)$$

where $Z = (F + M)$, and F is the instantaneous fishing mortality rate and M is the instantaneous natural mortality rate. Survival of the berried females is given by the equation:

$$N_{t_L} = N_j e^{-M(t_L - j)}, \quad \begin{array}{l} j = 1, 3, 5, \dots \\ j + 1 \geq t_L > j \end{array} \quad (3)$$

Values of M utilized herein were .10 and .15 as suggested by Wilder (1965).

At the outset we have two numerical coefficients for the females— N_0 for the non-berried and N_1 for the berried, where N_1 is the number of survivors from the first year of the non-berried state. The latter decay according to equation (3). Non-berried females decline according to equation (2).

Since in the case of females we are using the survivors of the non-berried state, unchanged in size, as the new N_j we are affecting a transformation of axis. The effect of this transformation is a shift of the curve for the berried females a (t_L) unit interval to the left so that we may write for the females over the interval from $0 \leq t_L \leq j + 1$

$$N_{t_L} = N_0 e^{-Z t_L}, \quad 1 \geq t_L \geq 0$$

$$N_{t_L} = N_1 e^{-M(t_L - 1)}, \quad 2 \geq t_L > 1$$

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$$N_{t_L} = N_{(j-1)} e^{-Z(t_L - (j-1))}, \quad j \geq t_L > j - 1$$

$$N_{t_L} = N_j e^{-M(t_L - j)}, \quad j + 1 \geq t_L > j$$

To find the average number of berried female survivors over a period (a, b) we must solve the equation:

$$\bar{N} = \frac{N_0}{b-a} \int_a^b f(t) dt$$

Since $f(t)$ is a sectionally continuous function it is necessary to find the average number of survivors over each period so that:

$$\bar{N}_k = \frac{N_j}{1-0} \int_0^1 e^{-Mt_L} dt_L \quad k = 1, 2, 3, 4, 5$$

$$j = 1, 3, 5, \dots$$

The integrated form of equation (4) is simply $\bar{N} = Na$ over M for each of the segments where a is the annual mortality rate and $a = 1-e^{-M}$. The average abundance during the year for each length is the area under the curve divided by the base (which is unity). The total fecundity of the lobster stock under various conditions of natural and fishing mortality rates can be found by multiplying the average abundance of each size class of berried females by its fecundity and summing for the entire population. The equation used to determine fecundity was derived from Herrick's (1911) data and is as follows:

$$\log Y = 0.70813 + 3.35462 \log X$$

where Y is fecundity and X is the total length. The logarithmic transformation was used because the relationship, when plotted graphically, was of the form $Y = ax^b$.

Sex ratios can easily be determined at any point on the curves by calculating the length of the ordinate for males versus that for total, berried and non-berried females.

MODEL RESULTS

Fig. 3 illustrates a family of sectionally continuous curves which were obtained with a total annual mortality rate of 60 percent acting equally on all classes of lobsters. From this figure it is apparent that the curve for males is continuous, but that the other curves are sectionally continuous as described in the model. It is also apparent that the decline in the numbers of all classes is extremely rapid and that only a small fraction of the total females remains at a total length of 15.2 inches (carapace length \sim 5 inches). This length is achieved after the fourth molt in the case of the model stocks under the assumptions of maturity at 9 inches and a 14 percent total length increase per molt. Fig. 4 illustrates the same total mortality rate (60 percent) but in this case a natural mortality rate of .10 is applied to the females which are protected in the berried condition. Only a slightly larger number of female lobsters remains in the stock after the completion of four molts.

In view of the significance of the numbers of females remaining after the completion of four molts for the double-gauge regulation, the results of all computations under various conditions are summarized in Table 1. From this table it is evident that the percentage of mature females remaining under realistic assumptions of total mortality is insignificant. In spite of increased fecundity with increasing size the total contribution of these larger animals to the total fecundity of the stock is very small. Under conditions of no protection of berried females these percentages are completely negligible. This is

obviously due to the fact that the total instantaneous mortality coefficient is effectively doubled for females at each mortality rate due to reduced molt frequency. These inferences from model data are essentially similar even if

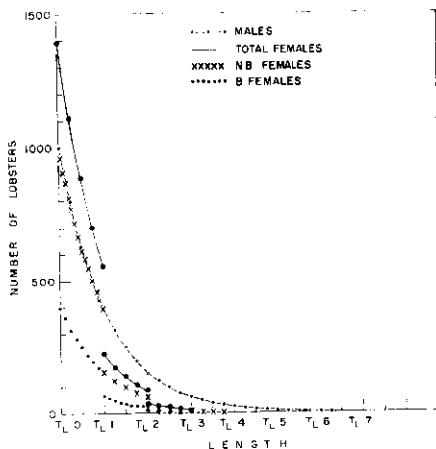


FIG. 3. The composition of a model lobster stock based on a uniform recruitment of 1000 males and 1000 non-berried females at maturity with a 60 percent total mortality rate and no protection of berried females.

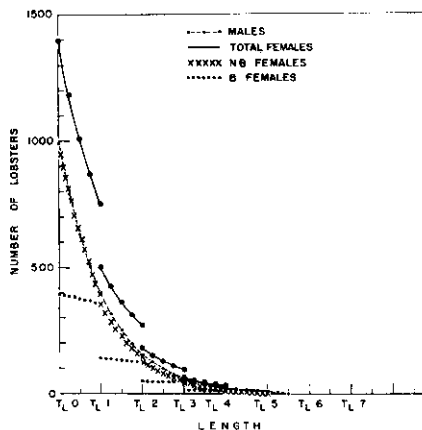


FIG. 4. The composition of a model lobster stock based on a uniform recruitment of 1000 males and 1000 non-berried females at maturity with a 60 percent total mortality and protection of berried females which have a 10 percent natural mortality rate in the berried condition.

a smaller size at maturity is utilized and also if the molt frequency of larger animals is reduced. Indeed, the results displayed in Table 1 are a conservative portrayal of the situation which probably pertains in nature.

TABLE 1

THE PERCENTAGE OF FEMALE LOBSTERS REMAINING IN THEORETICAL STOCKS UPON COMPLETION OF FOUR MOLTS AFTER MATURITY UNDER VARYING MORTALITY RATES, WITH AND WITHOUT PROTECTION OF BERRIED FEMALES.

	Total Mortality					
	.30	.40	.50	.60	.70	.80
Protection						
.10 natural mortality	33.5	17.7	8.6	3.5	1.1	0.2
.15 natural mortality	26.9	14.2	6.9	2.8	0.9	.17
No protection	9.0	4.3	1.1	0.2	0.03	0.00

The results of the model computations for various natural and total mortality rates with and without protection of berried females may also be summarized by calculating the total fecundity of each model stock as described in the model definition. Table 2 describes the results of these computations. It is clear from an examination of this table that consistently higher total fecundity values for the model stocks are obtained by protecting the berried females under all conditions tested. This increase in total fecundity is usually more than double the value obtained for the unprotected stocks under comparable total mortality rates.

Although not readily apparent from Table 2, but suggested by Fig. 2 and 3 is the fact that a major contribution to the total fecundity of the model lobster stocks is made by females which are berried for the first time. In model populations which involve no protection of berried females this statement holds for all levels of total mortality examined. In the case of protection, the major contribution to total fecundity is made by the newly berried females at total mortality rates of 0.50 and greater.

TABLE 2

TOTAL FECUNDITY ($\times 10^6$) OF MODEL STOCKS OF 1000 FEMALE LOBSTERS UNDER VARIOUS LEVELS OF TOTAL MORTALITY WITH AND WITHOUT PROTECTION OF BERRIED FEMALES. TWO LEVELS (.10 AND .15) OF NATURAL MORTALITY WERE APPLIED UNDER THE CONDITIONS OF PROTECTING BERRIED FEMALES.

	Total Mortality					
	.30	.40	.50	.60	.70	.80
Protection						
.10 natural mortality	63.4	25.1	20.4	13.6	7.6	4.1
.15 natural mortality	43.8	22.1	17.9	11.7	7.0	3.9
No Protection	28.6	15.9	9.1	5.4	3.1	1.6

The interesting observations by Hughes and Matthiessen (1962) on mating behavior which indicate that a relatively short time (48 hours) is available for successful mating after molting by the female, and that large males are invariably unsuccessful in attempting to mate with smaller females, have a bearing on regulations pertaining to the female as will be demonstrated. Thomas (1955) has already presented some information on sex ratio changes of model European lobster stocks, but he considered only a limited number of cases in which there was no protection of berried females. In view of the above, a summary of average sex ratios during each intermolt period for a duration of five molts is presented in Table 3. Examination of Table 3 indicates a sex ratio greater than unity in favor of females under all conditions through the first molt. This is, of course, due to the fact that mature females are in the first size class for effectively twice the length of time as mature males after recruitment, and the females are augmented by the survivors from the previous year's recruitment.

TABLE 3

SEX RATIOS (TOTAL FEMALES TO MALES) OF MODEL LOBSTER STOCKS AT FIVE SUCCESSIVE MOLTS FROM THE ONSET OF MATURITY UNDER VARIOUS CONDITIONS OF TOTAL MORTALITY AND PROTECTION OF BERRIED FEMALES.

Molt		Total Mortality					
		.30	.40	.50	.60	.70	.80
1	.10 P*	1.82	1.77	1.72	1.67	1.62	1.55
	.15 P**	1.78	1.74	1.69	1.65	1.59	1.52
	N P***	1.70	1.59	1.49	1.39	1.29	1.19
2	.10 P	1.64	1.60	1.55	1.51	1.46	1.40
	.15 P	1.50	1.47	1.43	1.39	1.34	1.29
	N P	1.19	0.95	0.75	0.56	0.39	0.24
3	.10 P	1.47	1.43	1.40	1.36	1.31	1.26
	.15 P	1.27	1.24	1.26	1.17	1.14	1.09
	N P	0.84	0.57	0.37	0.22	0.12	0.00
4	.10 P	1.32	1.29	1.26	1.22	1.18	1.13
	.15 P	1.08	1.05	1.02	0.99	0.96	0.92
	N P	0.59	0.34	0.19	0.09	0.03	0.00
5	.10 P	1.19	1.16	1.13	1.10	1.06	1.02
	.15 P	0.91	0.89	0.87	0.84	0.81	0.78
	N P	0.41	0.20	0.09	0.04	0.01	0.00

.10 P* = Protection of berried females with a 10 percent natural mortality rate in the berried condition.

.15 P** = Protection of berried females with a 15 percent natural mortality rate in the berried condition.

N P*** = No protection of berried females.

However, by the second molt the sex ratio becomes less than unity in all cases of no protection except at the lowest total mortality of 0.30. Note also that the sex ratio quickly becomes a very small decimal fraction in successive molts under all conditions except the lowest total mortality rate with no protection of berried females.

TABLE 4
COMPUTATIONS OF SURPLUS PRODUCTION FOR RHODE ISLAND INSHORE LOBSTER STOCK

	Catch Y 10 ³ lb	Effort f 10 ³ pots	Catch per pot Y/f lb	Fishing rate p	Mean stock \bar{W} 10 ³ lb	Initial stock W 10 ³ lb	Change ΔW 10 ³ lb	Surplus Production Y' 10 ³ lb
1942	427.5	11.5	37.2	1.57	272.3	231.6	-58.6	233.4
1943	292.0	11.2	26.1	1.53	190.8	173.0	+ 0.5	234.7
1944	234.2	11.1	21.1	1.51	155.1	173.5	+14.7	281.4
1945	266.7	10.2	26.1	1.39	151.9	188.2	+ 1.2	361.0
1946	359.8	14.3	25.2	1.85	184.5	189.4	- 1.0	391.7
1947	392.7	14.8	26.5	2.02	194.4	188.4	-22.5	360.3
1948	382.8	15.4	24.8	2.10	182.3	165.9	-22.1	332.5
1949	354.6	17.4	20.4	2.37	149.6	143.8	+13.2	263.2
1950	250.0	13.3	18.8	1.81	138.1	157.0	+ 3.4	214.5
1951	211.1	8.8	24.0	1.20	175.9	160.4	- 3.5	117.9
1952	91.2	4.6	19.8	0.63	144.8	152.2	+20.0	170.1
1953	121.4	5.6	21.7	0.76	159.7	148.7	+18.4	234.1
1954	150.1	8.0	18.8	1.09	137.7	168.7	+37.7	233.1
1955	215.7	7.9	27.3	1.08	194.7	187.1	+26.9	287.5
1956	199.4	8.2	23.8	1.12	174.5	224.8	-26.2	267.4
1957	260.6	7.0	37.2	0.95	274.3	251.7	+34.8	407.1
1958	293.6	9.4	31.2	1.28	229.4	225.5	-28.5	192.4
1959	372.3	12.3	30.3	1.68	221.6	260.3	-20.2	259.8
1960	430.6	10.6	40.6	1.44	299.0	231.8	- 1.19	257.9
1961	212.6	9.5	21.4	1.30	163.5	211.6		
1962	259.8	7.3	35.6	1.00	259.8	209.7		
1963	167.6	7.7	21.8	1.05	159.6			

DISCUSSION

The evidence available from the direct estimation of the relationship between stock density and surplus production is admittedly inconclusive, but some suggestion of a relationship between stock density and surplus production five years later was indicated. It should be pointed out that the Canadian data cited which concludes there is no convincing evidence in favor of regulations for protecting egg-bearing females is very tentative especially in view of the difficult sampling and estimation problems recently pointed out by Paloheimo (1963). It is apparent that other information must be assessed in order to obtain further insight concerning the regulation relating to egg-bearing females.

Model studies of lobster stocks which demonstrate the percentages of large females remaining at a carapace length of approximately 5 inches clearly show that there is no biological justification for the double-gauge regulation which involves protection of all large females. In spite of the fact that the fecundity of these large females is about an order of magnitude greater than that of females at first maturity, their contribution to the total fecundity of model stocks is significant only at low total mortality rates which do not appear to be realistic if the exploitation estimates of Wilder (1965) and Paloheimo (1963) apply in general. If it is postulated that the survival of eggs from extremely large females is lower than for the smaller specimens, then there is even less justification for their protection. One of the results of the model studies has been to clearly indicate the desirability of experimental studies on the relative survival of progeny from the entire range of sizes of egg-bearing females under controlled conditions.

The model data indicate consistently higher total fecundity values for model lobster stocks which are protected in the berried state. Although Wilder (1965) concluded that there probably wasn't any relationship between the abundance of egg-bearing females and commercial production, let us further consider the theoretical fecundity increase achieved by protecting berried females. From other investigations, Wilder (1947, 1963, 1965) has indicated that the movements of lobsters are limited (approximately 7 miles). These studies also showed little evidence for emigration or immigration from defined fishing grounds, and suggested that environmental factors such as temperature, habitat, food, competition, predation and possibly disease play an important role in determining the yield from a given region. If we accept the existence of local discrete groups of lobsters unaffected by emigration or immigration and a significant effect of environmental variables acting randomly on various life history stages of each group, then we may reasonably infer that lobster stocks with the highest total fecundity will also provide, on the average, the largest number of recruits when considered over a sufficiently long period of observation!

The average sex ratios obtained from the model studies indicate relatively stable values near unity for all combinations of mortality coefficients when protection is imposed on berried females. However, with no protection sex ratios rapidly decline to small fractions of females at the larger sizes. This model observation is of considerable interest in itself, since no previous work with marine organisms of economic importance has indicated such dramatic changes in sex ratios under presumed non-selective exploitation. In addition, if the laboratory observations of Hughes and Matthiessen (1962) showing that smaller males compete for the right to mate with larger males; with larger

males driving off the smaller males and that the mating of a large male with a smaller female is invariably unsuccessful hold in nature, then the probability of unsuccessful matings is significantly increased with sex ratios greatly in favor of males. Obviously, further field and laboratory studies of these phenomena are necessary. However, the stability of sex ratios is considered to be a point in favor of protecting berried females at this stage of our sex behavioral knowledge of the lobster.

The major argument in favor of this simple model of lobster stocks is that such model building helps to clarify the mechanism of a phenomenon, and thereby shows which attributes of a factor make the factor important as a regulating agent. An additional benefit, in this instance at least, has been the clear indication of what kinds of biological observations and experiments are required for a better understanding of the phenomenon in question. We submit also that our model has allowed us to demonstrate results which are not immediately apparent from the assumptions built into the model nor from available observational information.

SUMMARY

The results of direct estimation of the relationship between stock density and surplus production are demonstrated and considered inconclusive.

The theoretical effects of the double-gauge regulation are demonstrated for model stocks. No justification for this regulation is apparent from model studies.

A consistent increase in the total fecundity of model stocks which incorporated protection of berried females was demonstrated.

Stable sex ratios near unity were achieved with theoretical stocks which involved protection of berried females. A rapid decline of sex ratios in favor of males was demonstrated for unprotected females.

The high desirability of certain biological data not presently available was indicated from the model studies.

The advantage of model studies for inferences concerning biological phenomena which are extremely difficult to assess in natural stocks was demonstrated.

APPENDIX I

The values of p were obtained by using an annual fishing mortality rate ($m = .65$) for 1963, the base year. This value was derived from tagging data. The other values of p were estimated as proportional to effective fishing effort ($p_i = cf_i$ for each year).

The asymmetrical surplus production curve was fitted by estimating maximum surplus production as 340.0×10^3 pounds taken at a stock density of 220.0×10^3 pounds. The following two equations were solved simultaneously:

$$\frac{340.0}{P_r} = \frac{220}{P_r} e^{a(1-220/P_r)} - \frac{220}{P_r}$$

$$(1-220 a/P_r) e^{1-220/P_r} = 1$$

where $a = P_r/P_m$ and $P_r =$ parental abundance of prey which results in replacement reproduction and $P_m =$ parental abundance of prey which results in maximum reproduction.

The solution to these simultaneous equations is:

$$a = 1.54$$
$$P_r = 557.9$$

This is the solid curve drawn in Fig. 2. The notation of Ricker (1958) was utilized in the appendix to facilitate comparison with his text example.

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