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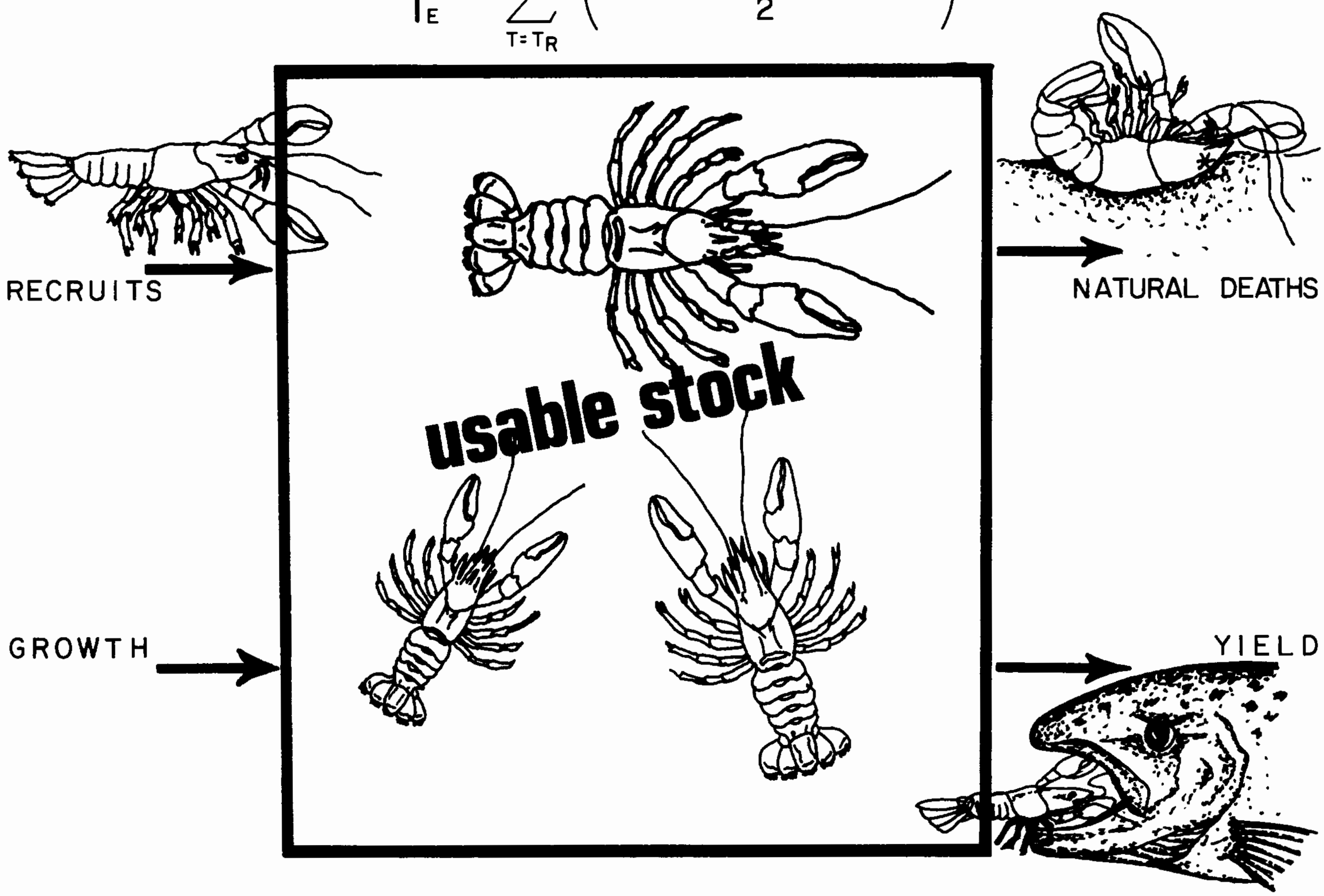
BY WALTER T. MOMOT & HOWARD GOWING

$$Y_E = \sum_{T=T_R}^{T=T_\lambda} \left(\frac{P_T \, W_{T(0)} \, (1 + e^{g_T - i_T})}{2} \right)$$



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By Walter T. Momot[2] and Howard Gowing

ABSTRACT

The Ricker model of equilibrium yield, programed for the computer by Paulik-Bayliff (1967), prescribed a sustained yield of crayfish in two small limestone sink lakes (located in the Pigeon River Area, Otsego County, Michigan). A crayfish fishery was created subject to specific regulations. The fishery developed according to theory. After the initial high first-year yield in West Lost Lake, the subsequent harvest decreased, then stabilized. Similar fishing regulations in North Twin Lake during the first 2 years resulted in an underharvest. The computer model prescribed a minimum 2-fold increase in fishing effort. Doubling the effort increased the harvest 1.5-fold and, in the fourth year, produced a yield comparable to those of the first 2 years.

The biotic response, of an unexploited population of crayfish to exploitation, subsequently showed (1) both an increase in the proportion of young animals in the population, and an increase in their growth, and (2) a decrease in annual production of the population. Egg production and recruitment did not respond.

The exploited crayfish population adjusted mainly through change in survivorship rather than a change in fecundity. Lack of a response in egg production was due to the selective nature of the fishery for males. By selectively fishing for males, the relative and absolute proportion of females in the population increased. Unexpectedly, the increase in females eventually resulted in low recruitment to the exploited stock.

Greater numbers of age-0 recruits were consistently produced in West Lost Lake than in North Twin Lake due to the greater annual availability and quality of the microhabitat.

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Introduction

Statistical techniques have greatly increased the study of population-regulating mechanisms in natural animal populations. Knowledge of such mechanisms is necessary to formulate sound strategies for optimum yield.

Animal populations in the laboratory have been used to derive theoretical approaches to optimize yield from a given level of production (e.g., Ketchum et al., 1949; Nicholson, 1955; Silliman and Gutsell, 1957, 1958; Silliman, 1968, 1972; Slobodkin and Richman, 1956; Watt, 1955).

Alternatively, data on commercially or recreationally exploited populations have been analyzed to formulate optimum yield strategies (e.g., Murphy, 1967; Schaeffer, 1968; Patriarche, 1968; Fox, 1970; Wise, 1972).

In addition, existing statistical data have been used to construct models of artificially generated populations, and by use of the computer to derive strategies for optimum yield (e.g., Larkin, 1963; Silliman, 1969; Paulik, 1969). Our approach is a modification of the last two methods. We had prior knowledge of the population dynamics of an unexploited species (Orconectes virilis) in a natural body of water. Since our crayfish harvest could be completely regulated, we were able to formulate a maximum yield strategy, evaluating it in terms of both yields and the effects which exploitation may have had on population dynamics and production. Also, we assessed the extent to which previously unexploited populations conform to predicted exploitation theory (Ricker, 1958).

There are several reasons for using crayfish as the target organism. Crayfish are the largest and longest-lived of North American freshwater crustaceans. As primary consumers in many environments, they account for the bulk of the intermediate production. Some of the larger species--among them Orconectes virilis--are of commercial importance (Avault, 1973; Power, 1962; Broom, 1963; LaCaze, 1966). Key aspects of their production ecology can be readily measured.

Study Area and Methods

The study site consisted of two lakes, West Lost and North Twin, located in the Pigeon River State Forest in the northcentral portion of the Lower Peninsula of Michigan, about 86 km south of the Straits of Mackinac (Fig. 1). These small landlocked lakes provide a simple natural ecological system for the study of animal populations. They are similar in geologic origin, size, morphometry, and water chemistry (Table 1). In 1966 they were designated as research waters closed to public fishing. Between 1966 and 1969, West Lost and North Twin lakes were the sites of a study by the authors involving the population dynamics of *Orconectes virilis*, and a report on that study is in preparation for publication. The present research, conducted from May 1970 to September 1973, also draws upon the earlier work of 1966-69.

Crayfish were collected with baited wire traps and nets. Analyses of such collections can indicate size, age, and density of the population (Momot, 1967a and 1967b). Estimates of crayfish were made by the mark-and-recapture method during non-molt periods, and were computed by the Schumacher-Eschmeyer (1943) multiple-census formula. Crayfish can be given an easily recognizable mark without harm, by excision of one or more pleura (Goellner, 1943; Momot, 1967a, 1967b). The accuracy of the estimates was corroborated by comparison with results derived by the DeLury method (DeLury, 1958).

Age composition was analyzed from size-frequency graphs in two ways: (1) by following the growth of size ranges of known-age animals (Momot, 1967a) and (2) by using arithmetic probability paper in a method described by Hopkins (1967). Carapace length was measured to the nearest millimeter using vernier calipers. Size-frequency polygons, using length of the cephalothorax plotted in millimeter intervals as the abscissa and the number of individuals as the ordinate, were used to separate the population into natural size groups with distinct, easily followed modes (Van Deventer, 1937; Hopkins, 1967). A series of size-frequency graphs, plotted at

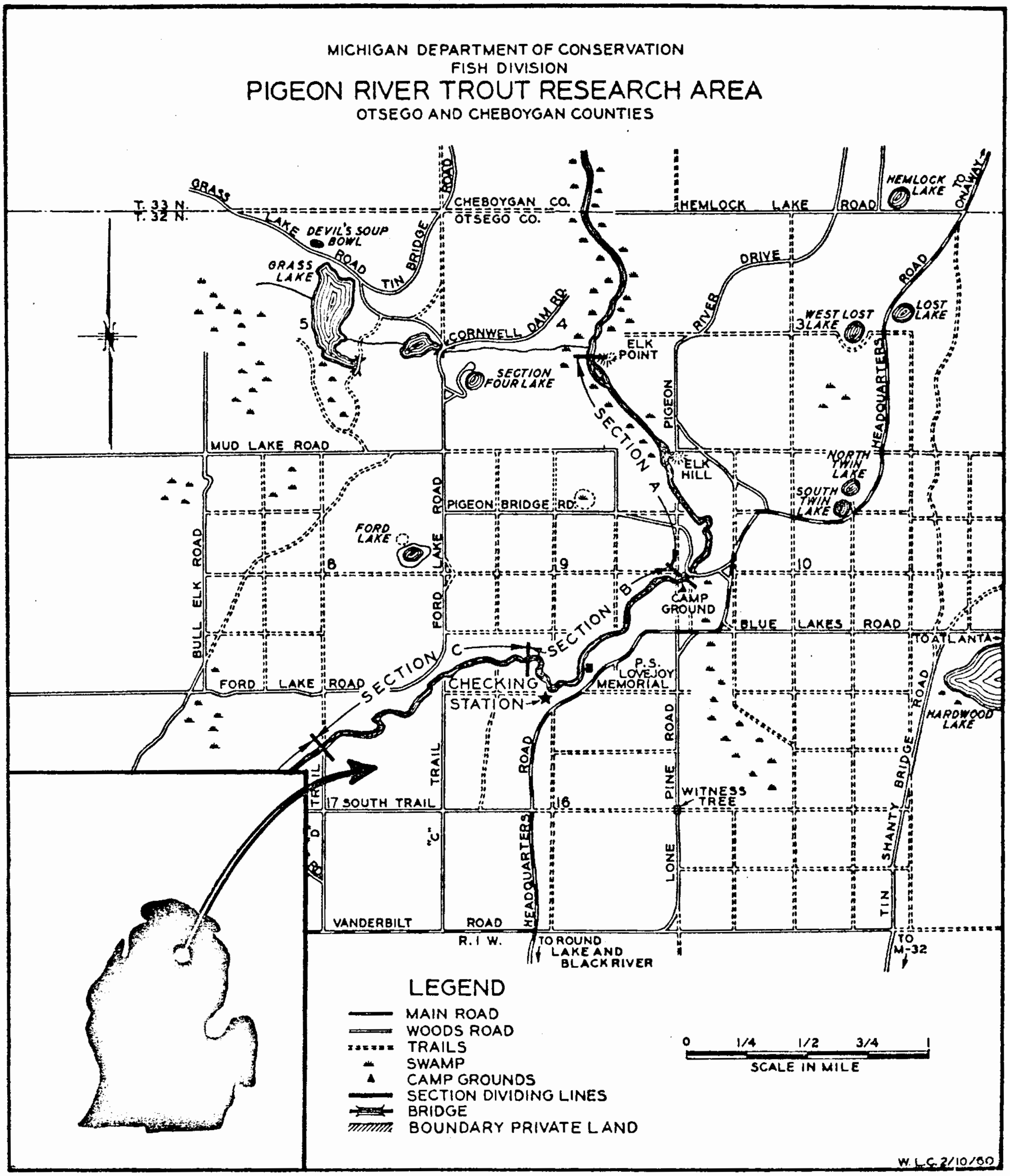

Figure 1.--Map showing location of study lakes.

Table 1. Limnological characteristics of two Pigeon River Area lakes (Tanner, 1960; Gowing and Momot, 1974).

Lake	Surface area (ha)	Depth (m)		Average total alkalinity (ppm)	Percentage shoal area <2.2 m	Total shoal area <2.2 m (m^2)
		Maximum	Average			
West Lost	1.4	13.1	8.5	134	20.1	2819
North Twin	1.9	12.5	8.2	29	19.6	3834

intervals within the growing season, provided an estimate of the rate of growth; age assessment was determined from the same graphs.

Seasonal growth in weight was determined from the series of samples used for population estimates. Length was converted to weight by use of a length-weight regression computed from empirical data. The natural logarithm of the ratio of the average final weight to the average initial weight for a unit of time was used to calculate the instantaneous rate of growth.

Reproductive success was determined from counts of eggs carried by females. Recruitment was determined by population estimates, made in the autumn, of young-of-the-year crayfish which had hatched in the spring.

Sequential population estimates were used to calculate the instantaneous rate of natural mortality (Ricker, 1958).

Production was calculated from instantaneous mortality and growth data derived from field observations (Ricker, 1958). Recently Chapman (In Gerking, 1967) summarized the development of fish production estimates and outlined the Ricker method. This method, when applicable, is superior to the Beverton and Holt model (Paulik and Bayliff, 1967). The model was particularly suitable for crayfish, since both growth and mortality nearly approximate exponential functions.

Prior knowledge of growth obtained from studies made between 1966 and 1969, and of mortality obtained during the first harvest, enabled us to determine the optimum yield harvest rate for each population in the two study lakes by using the Paulik-Bayliff (1967) computer program. Since no previous fishery existed prior to the study, we "created" a fishery subject to certain regulations. Initially, 30 baited minnow traps were fished for a period of 5 consecutive days (24-hour periods) in late August, giving us a total effort of 150 trap-days in the two lakes. During this period all crayfish less than 30-mm cephalothorax length were returned to the lake and those larger than this were removed. The 30-mm cephalothorax length protected the female brood stock, yet removed surplus males, the majority of which were age-II animals. As exploitation began, these regulations produced an optimum yield harvest in West Lost Lake but an underharvest in North Twin Lake. The computer model prescribed an effort of at least 300 trap-days for North Twin. Therefore, in North Twin Lake during the last 2 years of this study (1972-1973), we harvested crayfish using 60 traps for a 5-day interval. On West Lost Lake during this period, 1972-1973, we harvested crayfish at the initial effort of 150 trap-days.

Results

Harvest

Males comprised most of the crayfish harvested in these lakes. In West Lost Lake, after obtaining the estimates of summer adults, we began our harvest of crayfish in the last week in August 1970. The harvest consisted of age-I, age-II, and age-III males, with the latter two groups comprising 78% of the total (Table 2). Females constituted only a small fraction of the total catch. Initially 5,071 males were eligible for harvest (Table 2). After the first year (1970) the population of adult male crayfish stabilized at 3,306 to 3,316 (Table 2).

Initially in 1970 we harvested 2,995 male crayfish. This amounted to 58% of the resident population. The catch remained quite stable from 1,139 to 1,431, during the following 3 years. This represented 34% to 42% of the resident males. With a harvest effort of 150 trap-days, we achieved a sustained yield. The Paulik-Bayliff program confirmed that our present fishing effort of 150 trap-days was near the maximum sustained yield in West Lost Lake (Table 3).

In 1970, we fished North Twin Lake at the same intensity (150 trap-days) as in West Lost Lake. There were 3,141 male adults in North Twin. Age-II and age-III male crayfish comprised 92% of the catch (Table 2). Females were slightly more vulnerable to harvest in North Twin but still comprised a negligible fraction of the catch. Again, the size selectivity of the traps and the 30-mm size limit excluded most of the adult females

Table 2. Harvest of male and female crayfish 30 mm and larger (carapace length) after 150 trap-days (30 traps × 5 days) in West Lost and North Twin lakes in the summers of 1970 and 1971; 150 trap-days in West Lost and 300 trap-days in North Twin during 1972 and 1973.

Year, sex, and age group	West Lost Number Available	West Lost Number Harvested	West Lost Percent	North Twin Number Available	North Twin Number Harvested	North Twin Percent
1970						
Male						
I	2459	656	26	1756	68	4
II	2576	2305	89	1369	775	57
III	36	34	94	16	17	100
	5071	2995	58	3141	860	27
Female	3989	15	<1	2401	45	2
1971						
Male						
I	1694	309	18	1611	183	11
II	1588	1103	69	1113	676	61
III	34	19	56	40	34	85
	3316	1431	42	2764	893	32
Female	4945	106	2	4495	30	<1
1972						
Male						
I	1688	188	11	1462	406	28
II	1442	931	65	1576	898	57
III	183	125	68	41	13	32
	3313	1244	38	3079	1317	43
Female	6865	5	<1	5440	96	2
1973						
Male						
I	1942	370	19	1915	115	6
II	1294	741	57	1293	641	50
III	70	28	40	185	79	43
	3306	1139	34	3393	835	25
Female	3470	72	2	4697	59	1

from harvest. The harvest in 1971 was continued with the same effort (150 trap-days). The available population of adult males was only slightly smaller (2,764 crayfish) than in 1970. The harvest was approximately the same in both years: 860 in 1970, and 893 in 1971. This amounted to removal of 27% of the population in 1970 and 32% in 1971. Hence, this 2-year period produced a sustained catch. The fishing and natural mortality rates used in the Paulik-Bayliff program resulted in an underharvest of the crayfish resource in North Twin. Therefore, we doubled the fishing effort in this lake in 1972 (Tables 2 and 3), to 300 trap-days, by fishing 60 traps for 5 days.

The Paulik-Bayliff program showed that yields increased continuously at each increase in effort (Table 3). There was not a "peak" effort followed by a severe decline, as is shown for yield-isopleths plotted for many fisheries. Instead, a plateau was reached at a fishery effort multiple of 2.00-3.00, after which the yield increased at a slower increment with increased effort. Hence, we concluded that for maximum efficiency, harvest should take place immediately after a peak biomass for a given cohort (year class) is reached and that the surplus should be harvested at the lowest possible effort. This was felt to be two to three times the present effort; thus we conservatively chose a 2-fold increase in effort in North Twin. Fortunately, at the level fished, catch per unit of effort was somewhat proportional to fishing mortality. Thus, in 1972, with effort at 300 trap-days, we harvested 1,317 males. This was 43% of the 3,079 resident adult males. Thus doubling the effort produced a 1.5-fold increase in the harvest. With the same intensity of effort in 1973, we harvested 835 males or about 25% of the 3,393 males available. Although effort was increased 2-fold in 1973, the harvest was about the same as in 1970 and 1971. The population of adult males was larger in 1973 than in any other harvest year, primarily due to the larger number of age-I males. In turn, we harvested only 6% of this age group in 1973, compared to 28% in 1972 (Table 2).

The harvestable population in North Twin increased slightly from 1972 to 1973. Hence, most of the decline in the actual harvest was caused by a decrease in the percentage which was harvested, especially of age-I

Table 3.- Yield matrices for the crayfish populations of West Lost and North Twin lakes. Age at entry and fishing effort multiple selected for optimizing harvest are underscored.

Year, lake and age at entry	Yield Kilograms per kilogram recruits							
1970								
West Lost								
3.5	1.422	1.524	1.560	1.575	1.592	1.599	1.604	1.606
2.5	1.583	1.601	1.603	1.603	1.602	1.601	1.601	1.601
1.5	1.536	1.529	1.509	1.489	1.433	1.372	1.322	1.282
Effort[1]	0.50	0.75	1.00	1.25	2.00	3.00	4.00	5.00
North Twin								
3.5	0.555	0.584	0.592	0.595	0.595	0.595	0.595	0.595
2.5	0.893	1.006	1.086	1.268	1.353	1.431	1.468	1.479
1.5	0.902	1.016	1.095	1.267	1.339	1.400	1.402	1.402
Effort	0.50	0.75	1.00	2.00	3.00	5.00	6.00	7.00
1971								
West Lost								
3.5	0.639	0.812	0.936	1.029	1.110	1.206	1.332	1.405
2.5	1.255	1.468	1.584	1.650	1.688	1.726	1.748	1.755
1.5	1.262	1.454	1.548	1.593	1.612	1.617	1.584	1.543
Effort	0.50	0.75	1.00	1.25	1.50	2.00	3.00	4.00
North Twin								
3.5	0.837	0.946	1.003	1.037	1.060	1.089	1.120	1.135
2.5	1.400	1.579	1.686	1.760	1.814	1.888	1.970	2.014
1.5	1.401	1.578	1.683	1.754	1.805	1.873	1.943	1.975
Effort	0.50	0.75	1.00	1.25	1.50	2.00	3.00	4.00

[1] Fishing effort.

males. This decrease in harvest of age-I males was coincident with a decrease in their mean length from 28.2 to 26.5 mm. Many age-I males were far below the size limit of 30 mm.

Changes in age composition

As a previously unexploited population is harvested, the percentage of younger animals in the population should increase. Since males comprised most of the exploited portion of the population, any change in age structure directly caused by fishing would be reflected among males.

The number of age-I male crayfish decreased after 1970 to levels generally below that of the pre-harvest years (Table 4). Since this age group was not subject to intense harvest, the decrease must have been due to other factors. Age-II and age-III crayfish were harvested intensively. Except for the unusually large population in 1966, the number of age-II males in West Lost decreased after 1970. North Twin showed no such trend for these age groups (Table 4).

Females were not subjected to intense harvest. Nevertheless, the average number and proportion of age-I females showed some increase in West Lost and North Twin during 1971, 1972, and 1973, compared to the years immediately preceding them (Table 4). Evidently, the selective fishery for males favored the survival of females from age 0 to age I, though this increase was also confounded by the production of poor year classes. However, the survival of females from age I to age II decreased during these years (1971-1973). This affected both recruitment and egg production as discussed below.

Fecundity

As an unexploited population is first cropped, older organisms are supposedly replaced by younger, more efficient ones. This lessening of intraspecific interactions within a population could increase egg production per female and perhaps total egg production. Egg production measured as the number of attached eggs per adult female failed to show any such response in either lake (Table 5). In North Twin Lake the mean number of attached

Table 4. Age group composition of the crayfish populations in West Lost and North Twin lakes from 1966 to 1973.

Lake, sex	Year	Age group 0	I	II	III
West Lost					
Male	1966	24,809	12,022	13,150	521
	1967	18,589	1,823	3,079	70
	1968	8,641	2,887	1,799	47
	1969	42,983	3,350	2,109	33
	1970	17,111	2,459	2,576	36
	1971	23,897	1,694	1,588	34
	1972	14,148	1,688	1,442	183
	1973	13,978	1,942	1,294	70
Female	1966	30,187	6,713	3,758	34
	1967	28,412	2,137	1,453	113
	1968	12,436	2,545	1,313	28
	1969	21,171	2,109	2,178	34
	1970	20,498	3,387	590	12
	1971	25,274	2,893	1,893	159
	1972	10,938	5,107	1,613	145
	1973	16,408	2,144	1,287	39
North Twin					
Male	1966	20,874	10,279	2,447	60
	1967	17,097	2,379	1,592	110
	1968	9,992	6,177	1,104	73
	1969	20,435	3,570	1,491	47
	1970	26,296	1,756	1,369	16
	1971	10,907	1,611	1,113	40
	1972	6,675	1,462	1,576	41
	1973	4,631	1,915	1,293	185
Female	1966	24,085	5,853	4,057	60
	1967	20,152	2,410	1,895	61
	1968	12,718	3,442	984	45
	1969	26,759	2,450	1,425	84
	1970	27,043	1,440	934	27
	1971	10,726	3,039	1,242	124
	1972	5,943	3,835	1,430	175
	1973	5,895	3,607	991	99

Table 5. The mean number of attached eggs per female crayfish, and the attached-egg production per square meter of littoral area, in West Lost and North Twin lakes from 1966 to 1973.

Lake and Year	Number of female crayfish examined	Egg counts		Egg production per square meter of littoral area
		Mean number	S.E. (±)	
West Lost				
1966	73	61.9	3.8	122.6
1967	42	64.8	5.6	92.4
1968	43	92.1	5.3	65.6
1969	52	78.4	5.5	83.3
1970	51	64.8	5.8	52.7
1971	62	39.4	4.8	55.7
1972	51	52.5	6.4	37.8
1973	42	44.4	5.7	30.5
North Twin				
1966	78	25.7	3.3	26.5
1967	54	68.0	5.5	46.1
1968	33	116.8	6.6	67.8
1969	37	82.1	8.3	34.9
1970	52	51.3	4.9	19.1
1971	33	56.2	7.2	30.7
1972	54	53.4	5.7	26.4
1973	54	42.2	4.9	17.4

eggs per adult female has been shown to be inversely related to density. Following exploitation, the population of sub-adult females has increased slightly in both lakes (Table 4). The biotic response to this crowding was a decrease in fecundity in the population (Table 5).

Growth

Older crayfish tend to convert a smaller fraction of the food they consume into flesh than do the young animals. As older crayfish are removed, intraspecific competition is reduced, resulting in an increase in growth rate of the younger crayfish. Since our exploitation mainly affected the male population, we would expect an increase in the growth of the younger age groups affected by the fishery. This was precisely what happened. The instantaneous growth rate of age-I males during the exploitation period was greater than during the pre-exploitation period; however, this was also true of age-I females (Fig. 2). Age-II females and age-II males showed little growth response to exploitation (Table 6). The general stability in density of age-II males resulted in a rather constant annual growth rate.

Recruitment

One of the biotic responses to exploitation expected from a previously unexploited population is an increase in the rate of recruitment. Recruitment is the addition of new members to the exploited stock by growth from smaller size groups, and by the addition of new members from reproduction. The latter is a function of the mean fecundity and the number of mature egg-bearing females present in the population at spawning.

An increase in recruitment failed to occur in these populations (Fig. 3). Number of eggs produced per square meter of the littoral zone generally diminished in both lakes during the period of exploitation (Table 5). This resulted from both a reduction in fecundity and the failure of the female brood stock to significantly increase in size (Tables 5 and 7). An increase in the population of sub-adult (age-I)

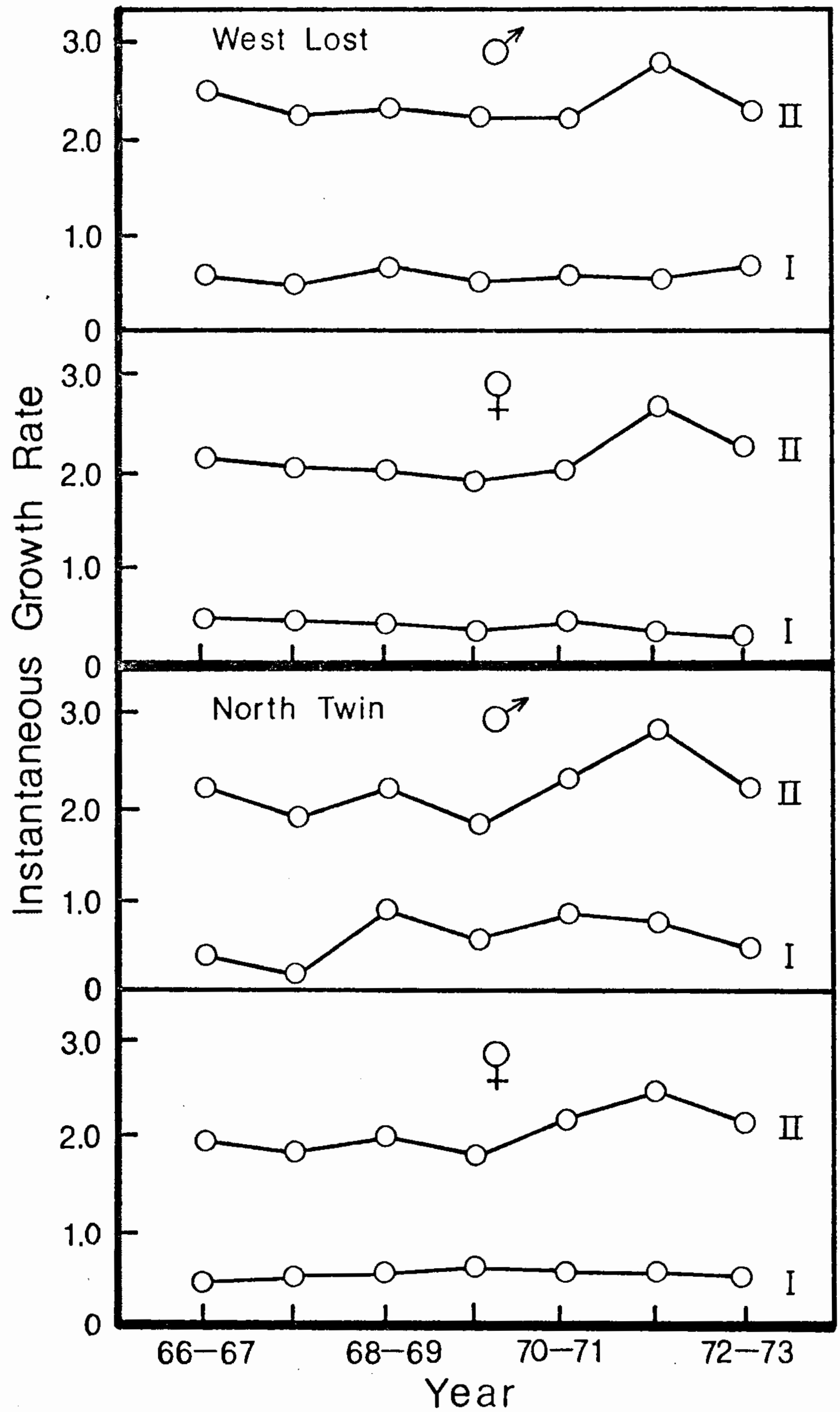

Figure 2.--The variation from 1966 to 1973 in the instantaneous growth rate (g) for age-I and age-II crayfish of each sex in West Lost and North Twin lakes.

Table 6. Carapace length (mean and standard error) of crayfish from West Lost and North Twin lakes during late summer.

Lake, year, and age group		Males			Females		
		Number	Length (mm)		Number	Length (mm)	
			Mean	S.E. (±)		Mean	S.E. (±)
West Lost							
1966	0	79	13.8	0.12	221	13.4	0.11
	I	437	26.9	0.09	1073	24.9	0.03
	II	467	31.8	0.10	962	28.2	0.04
	III	11	37.8	0.29	3	35.7	0.66
1967	0	162	14.3	0.12	263	13.8	0.10
	I	87	29.4	0.10	300	26.5	0.09
	II	296	32.8	0.08	203	30.0	0.06
	III	12	38.3	0.36	16	33.6	0.21
1968	0	142	14.3	0.15	199	13.9	0.11
	I	907	27.9	0.08	316	25.3	0.11
	II	574	35.2	0.06	166	31.0	0.12
	III	10	40.7	0.22	1	35.0	0.00
1969	0	73	13.3	0.19	137	13.1	0.13
	I	1423	29.3	0.05	400	25.6	0.07
	II	895	34.9	0.07	413	29.4	0.07
	III	13	41.1	0.08	6	36.3	0.18
1970	0	67	13.3	0.78	80	13.4	0.15
	I	1978	27.5	0.10	176	24.9	0.09
	II	2051	34.2	0.04	264	28.8	0.10
	III	50	40.6	0.11	6	36.8	0.54
1971	0	54	11.3	0.21	57	9.8	0.38
	I	977	27.5	0.05	695	25.5	0.05
	II	917	33.2	0.05	456	29.0	0.04
	III	17	39.7	0.16	37	32.4	0.09
1972	0	93	13.7	0.13	72	13.1	0.17
	I	1231	26.8	0.05	501	25.1	0.07
	II	1083	33.1	0.04	158	28.7	0.07
	III	136	38.0	0.10	14	32.8	0.24
1973	0	144	12.3	0.12	124	12.6	0.14
	I	1367	28.1	0.06	407	24.5	0.07
	II	916	33.7	0.06	244	27.9	0.07
	III	34	40.0	0.22	7	33.0	0.35

(continued, next page)

Table 6 (continued)

Lake, year, and age group		Males			Females		
		Number	Length (mm)		Number	Length (mm)	
			Mean	S.E. (±)		Mean	S.E. (±)
North Twin							
1966	0	130	16.3	0.14	150	15.5	0.14
	I	503	29.6	0.07	197	29.9	0.07
	II	75	34.6	0.19	5	35.4	0.51
	III	2	40.5	0.50	...	....	....
1967	0	134	15.3	0.16	158	14.5	0.14
	I	429	31.3	0.08	334	26.6	0.08
	II	288	34.4	0.07	262	30.4	0.09
	III	19	38.4	0.22	8	36.5	0.42
1968	0	130	13.4	0.12	160	12.9	0.11
	I	1214	26.1	0.05	647	24.9	0.08
	II	213	34.2	0.10	179	30.6	0.10
	III	17	39.1	0.24	8	35.9	0.98
1969	0	112	14.0	0.15	90	13.5	0.16
	I	620	27.2	0.09	656	24.6	0.06
	II	259	35.1	0.12	381	29.5	0.06
	III	8	42.7	0.57	22	36.6	0.24
1970	0	111	13.2	0.08	114	12.7	0.10
	I	1263	25.1	0.05	281	24.4	0.12
	II	985	33.4	0.07	182	29.7	0.11
	III	11	42.1	0.27	5	36.8	0.52
1971	0	60	11.8	0.16	59	11.7	0.16
	I	990	27.0	0.05	555	25.4	0.06
	II	684	33.2	0.06	227	28.8	0.06
	III	23	39.2	0.37	22	33.1	0.35
1972	0	62	12.9	0.16	55	12.8	0.03
	I	988	28.2	0.08	637	26.0	0.06
	II	1073	34.7	0.04	238	30.0	0.06
	III	20	40.6	0.17	28	33.7	0.21
1973	0	86	13.1	0.17	74	13.6	0.16
	I	1138	26.5	0.06	738	25.9	0.06
	II	777	33.3	0.05	203	29.9	0.07
	III	102	38.1	0.13	20	33.6	0.25

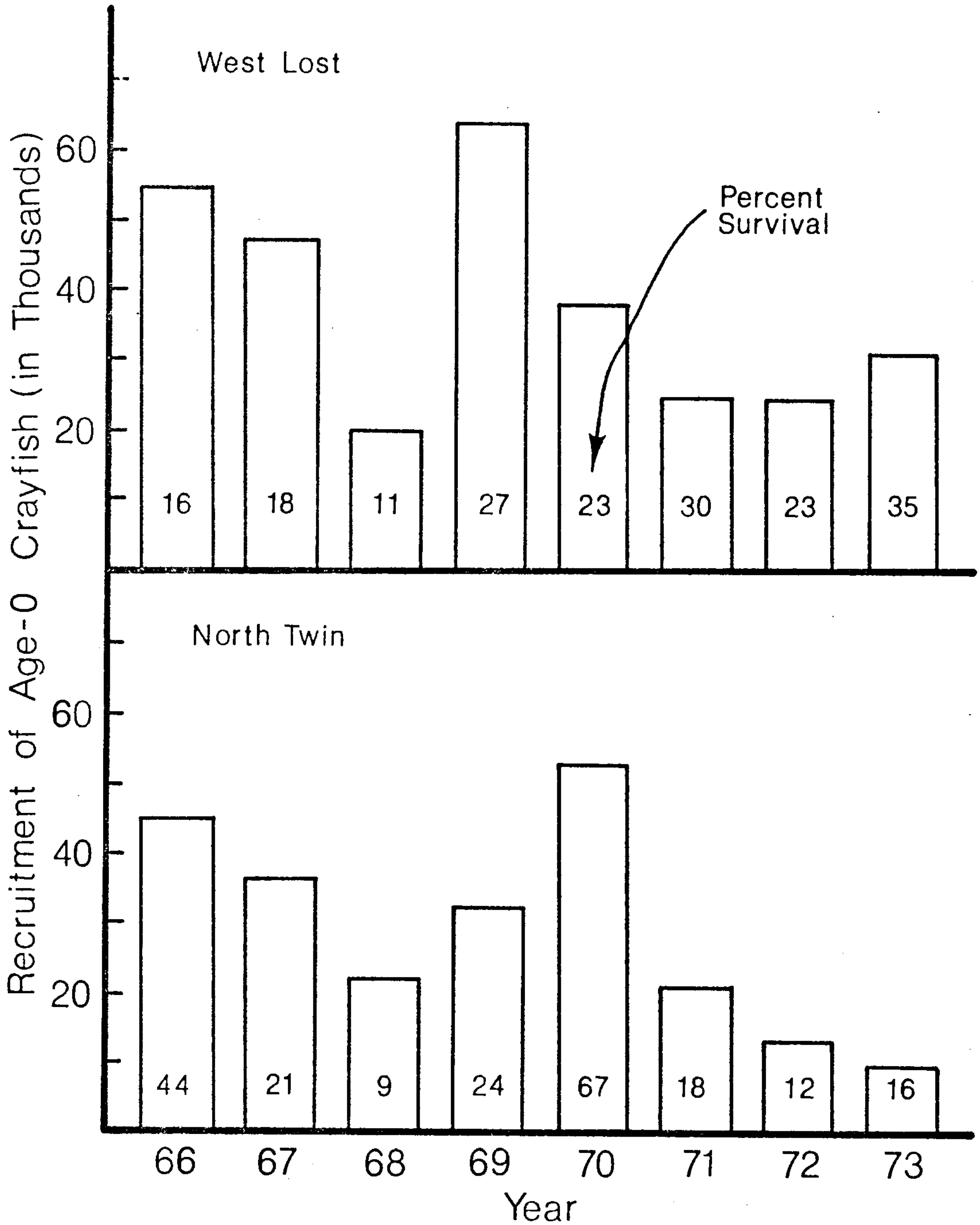

Figure 3.--Recruitment and percentage survival of crayfish during their first growing season in West Lost and North Twin lakes. Data presented as total number of age-0 crayfish present in late summer with percentage survival from hatching shown within each bar on the graph.

Table 7. Spring estimates of adult female crayfish in West Lost and North Twin lakes.

Lake and year	Age II	Age III	Total
West Lost			
1966	5289	297	5586
1967	3230	791	4021
1968	1903	105	2008
1969	2754	243	2997
1970	1608	684	2292
1971	2009	1977	3986
1972	1710	326	2036
1973	1801	139	1940
North Twin			
1966	4157	185	4342
1967	2021	577	2598
1968	2094	133	2227
1969	1432	199	1632
1970	1166	262	1428
1971	1751	346	2097
1972	1504	424	1928
1973	1432	154	1586

females may have led to competition for food which lowered mean fecundity per female (Table 4). Also the increase in number of age-I females failed to result in an increase in number of age-II females at the time of spawning (Tables 4 and 7). Because of this poor survival of age-I females to spawning size, there were only average populations of spawners (Table 7) and, with the lower mean fecundity, recruitment at hatching was below average (Table 5). In West Lost Lake the lower recruitment at hatching was somewhat compensated by a better than average survival of young-of-the-year to the end of their first summer's growth (Fig. 3). North Twin Lake showed a much poorer response, for survival of young to the end of first summer was less than average (Table 8).

Over the years of study, West Lost Lake consistently produced more age-0 recruits per hectare than did North Twin Lake. The key to this difference lay in the greater annual availability of microhabitat for young-of-the-year in West Lost Lake. The microhabitat of the young consisted entirely of beds of the emergent sedge *Carex aquatilis* var. *substricta*. During their first growing season, the young were found within and in the immediate proximity of these beds. The beds occupied the immediate shoreline of the lake, usually out to a depth of 0.5 m, and formed a concentric band around the circumference of the lake. A vegetative index (D) to the quality of this emergent vegetation was determined for 1969 and 1973. This index (D) was constructed as follows: first we selected sample sites at 10-m intervals around the circumference of the lake. At each sample site we measured on a perpendicular line the linear width in meters of the vegetation band from the water's edge to the end of the vegetation. The clumps of vegetation within this linear distance were counted. A clump was counted if any portion of it touched the perpendicular line used to measure the width. The index is computed as the product of the width of the band times number of clumps (Table 9). The year 1969 was considered to be our base year for comparison with 1973.

Table 8. Recruitment (R) of young-of-the-year crayfish at the end of the first growing season expressed as the number per square meter of littoral area.

Year	West Lost	North Twin
1966	19.5	11.7
1967	16.7	9.7
1968	7.5	5.9
1969	22.7	12.3
1970	13.3	13.9
1971	17.4	5.6
1972	9.0	3.3
1973	10.7	2.7

Table 9. Vegetative index (D) of the available microhabitat of young-of-the-year crayfish.

Lake, and year	A Number of samples	B Number of clumps per interval Mean	S.E. (±)	C Linear distance (m) of vegetation band Mean	S.E. (±)	B × C Vegetation index D	B/C Density
West Lost							
1969	44	5.07	0.50	0.976	0.098	4.94	5.19
1973	42	2.14	0.24	0.446	0.045	0.95	4.79
North Twin							
1969	54	3.65	0.40	0.601	0.690	2.19	6.07
1973	54	1.48	0.23	0.616	0.630	0.91	2.40

During the period of exploitation (1971-1973) the water level in the two lakes increased greatly, exceeding levels of 1968-1970, and inundated much of the emergent vegetation. This is reflected in the decrease in index values (D) in the two lakes (Table 9). The higher level affected both the density and the linear extent of the vegetative band. Whereas in 1969 West Lost Lake had a much higher D value, by 1973 it was nearly the same as in North Twin Lake. However, the density of the vegetation in West Lost was greater. The mean number of clumps per meter of width averaged 4.8 in West Lost, but only 2.4 in North Twin. Consequently, while the quality of the microhabitat declined in both lakes, it still was considerably better in West Lost than in North Twin (Table 9).

We also measured the influence of physical factors--notably temperature and mean monthly precipitation--on recruitment. No correlation was observed among these variables. We also examined the relationship of lake water level to three aspects of recruitment, as follows: (1) egg production per square meter of littoral area, (2) number of recruits per square meter of littoral area, and (3) percentage survival from hatching in spring until fall. Water level did not directly affect recruitment of year classes in the lakes. Water level could function in an indirect manner. Abrupt changes in water level can alter the microhabitat (*Carex* beds) both in quantity and quality, and under such conditions recruitment is abetted.

Ricker (1958) pioneered the concept of the reproduction curve in analyzing the effects of population density. In using reproduction curves, the abundance of the parental stock is compared with the abundance of the resulting progeny at spawning a generation later. Since age-II females comprise 90% of the spawning population, and age-III the remainder, the spawning stock was considered to approximate a single age group. In theory, reproduction curves represent the net effect of all the density-dependent factors acting upon a population. However, density-independent factors would tend to displace the reproduction curves and to obscure relationships somewhat. These curves are characterized as having an ascending limb, and dome, descending limb. The maximum height of the dome above a 45° slope, representing replacement reproduction, indicates the point of maximum recruitment. In general this line is supposed to occur at intermediate abundance levels. In theory, if the population of a single spawning stock is kept at the level of abundance where recruitment is maximum, then the population should produce a maximum yield at this density (Ricker, 1958). Each curve is drawn in relation to the 45° slope, in which filial generations are equal to parental generations. The curve, if it describes a population regulated by density-dependent factors, begins above the 45° slope and then crosses and ends below it. In general the reproduction curves for the crayfish in West Lost and North Twin lakes appear to have a flattened dome, with the curve for West Lost being higher than that for North Twin (Fig. 4). Since each curve represents only a single population, the most likely explanation is that we have populations limited by available space (Ricker, 1958). Flattening occurs when there is a fixed number of safe habitat niches available to the population. If the population exceeds what the habitat can accommodate, the surplus animals are lost. This explanation fits our hypotheses that the size and density of Carex beds are important in determining recruitment to the population, and that abundance of Carex beds is a limiting factor in the production of crayfish in the lakes.

In North Twin, maximum recruitment occurred at a population size of 4,300; however, this did not produce a replacement recruitment. Replacement occurred only when the size of the spawning stock fell below 1,500 (Fig. 4). In West Lost, the maximum recruitment occurred at spawning stock size of 4,000, but the resulting recruitment was less than replacement size. Replacement reproduction occurred at a spawning stock size of about 2,000, while recruitment in excess of replacement occurred at a spawning stock of less than 2,000 (Fig. 4). Apparently we have a population which is regulated extremely well, with the spawning stock being kept within fairly narrow limits. Poor survival of the 1968 year class, which occurred in both lakes, resulted in a bimodality of the curve at about 2,000 individuals. We believe that the curves are essentially flat. The deflection in 1968 was caused by some density-independent factor which depressed the curve. In the late fall of 1967,

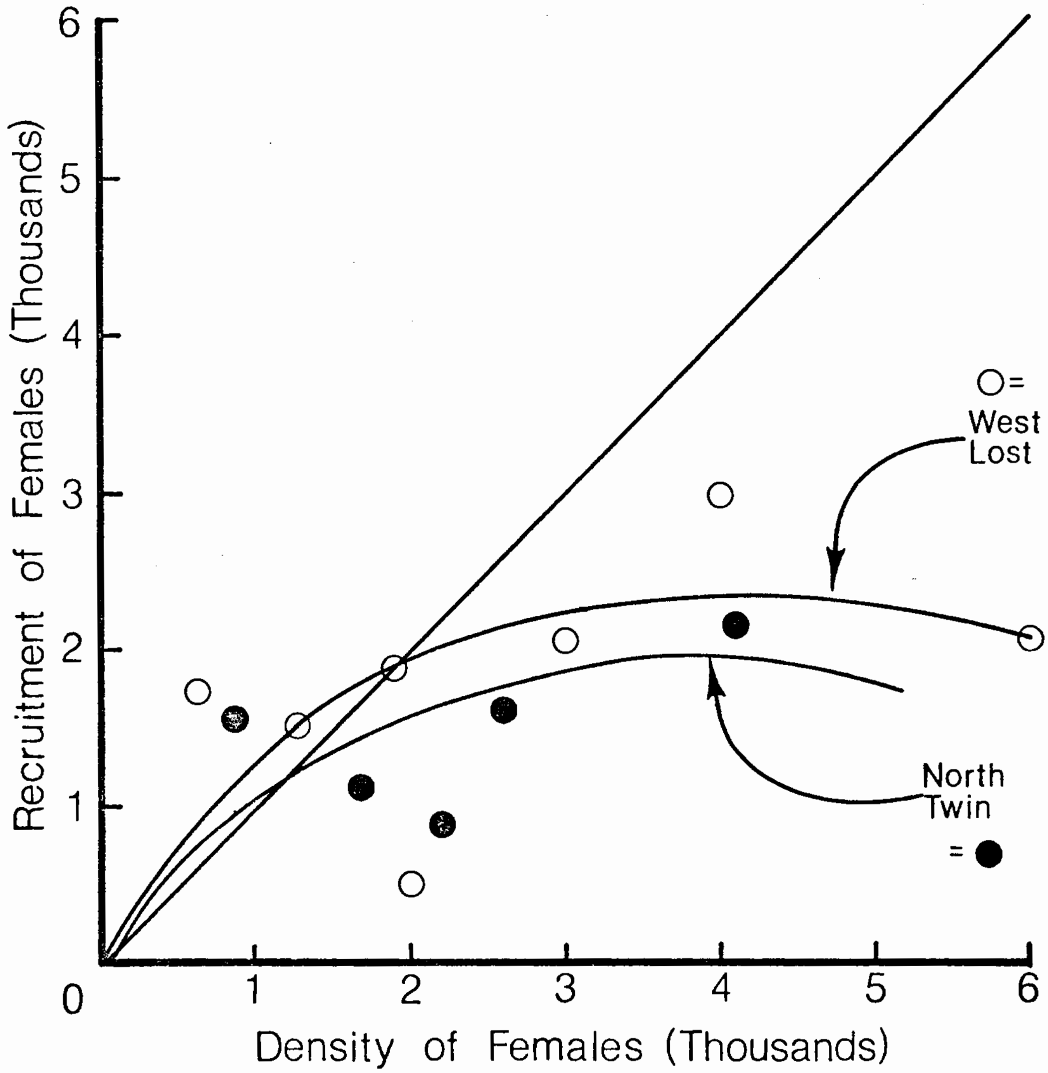

Figure 4.--Reproduction curve for crayfish in West Lost and North Twin lakes, showing the relationship between density of spawning females at age 2+ and the recruitment of age 2+ females 2 years later.

very high densities of large trout were stocked in these lakes. These fish preyed heavily on young-of-the-year hatched in 1968, especially in West Lost Lake (Gowing and Momot, 1974). No doubt this had some effect on the poor survival of the 1968 year class. The remarkable stability of these populations is reflected in the flat shape of the reproduction curves; the stability comes from very strong density-dependent controls regulating the populations.

Annual production, mean biomass and turnover ratio

Theoretically, exploitation replaces the older members of a population with younger individuals that are more efficient in converting food to new flesh. We should expect annual production and the annual turnover ratio of the population to increase during exploitation. The latter is defined as the production divided by the mean summer biomass. Annual production in North Twin Lake declined after 1970 (Table 10); in 1966-1970 it averaged 64.6 kg/ha, and after 1970 it has averaged 41.6 kg/ha. In 1966-1970 the mean biomass averaged 63.6 kg/ha; since 1970 it averaged 34.2 kg/ha. The mean annual turnover ratio for the pre-exploitation period (1966-1970) was 1.04, and after 1970 it averaged 1.20. In West Lost Lake during these same intervals, standing crops went from an average of 88.8 kg/ha, to 55.3 kg/ha; mean biomass remained rather constant at 51.7-58.7 kg/ha (Table 10). Annual production in West Lost during the pre-exploitation phase averaged 101.6 kg/ha. Once again the unusually good year of 1966 (133.8 kg/ha) inflated this average. Since exploitation began, mean annual production has been lower, averaging 64.8 kg/ha. The mean turnover ratio for the pre-exploitation period was 1.20; after exploitation it averaged 1.18.

Cohort production and turnover ratios

Benthic production can be compared on a life-cycle basis. To do this, it becomes necessary to calculate the cohort production and the cohort turnover ratio. The latter is defined as the ratio of a cohort's

Table 10. Mean summer biomass ($\bar{B}$), production (P), and the annual turnover ratio (TR = $P/\bar{B}$) of crayfish in West Lost and North Twin lakes.

Lake and year	$\bar{B}$ kg/ha	P kg/ha	TR
West Lost			
1966-67	142.9	133.8	0.94
1967-68	65.6	86.9	1.33
1968-69	71.9	94.9	1.32
1969-70	74.8	91.0	1.22
1970-71	58.7	61.3	1.05
1971-72	55.6	76.6	1.38
1972-73	51.7	56.6	1.10
North Twin			
1966-67	82.4	84.6	1.02
1967-68	49.9	60.2	1.20
1968-69	78.2	65.7	0.85
1969-70	44.1	47.8	1.08
1970-71	33.0	45.9	1.39
1971-72	33.9	43.7	1.28
1972-73	35.6	33.6	0.94

production to the mean standing crop determined over the life of that cohort. The cohort production prior to exploitation ranged from 53.6 to 108.5 kg/ha, while the cohort mean standing crops varied from 9.4 to 18.8 kg/ha (Table 11). The pre-exploitation turnover ratios were not especially variable, ranging from 4.61 to 5.77 (Table 11). Beginning with exploitation in 1970, we derived cohort production values for only the 1970 cohort. Excluding the age-III crayfish for which we do not have data, the 1970 cohort turnover ratio was 5.28 for West Lost and 4.39 for North Twin. Thus, cohort production and turnover ratios were similar to the pre-exploitation period.

Post-exploitation production of age-0 male crayfish was slightly below that of the 1966-1969 period (Table 12). This was mainly due to poor recruitment of age-0 crayfish during the exploitation period, rather than to any drastic change in growth or mortality values used in the calculations.

Crayfish harvest strategy

Though widely distributed, crayfish are commercially harvested in only a few geographical areas of the United States (Avault, 1973). Minor commercial fisheries for crayfish are located on the West Coast of the United States (Miller and Van Hyning, 1970) and in Wisconsin (Threinen, 1958); whereas the major fishery is centered in the Bayou area of Louisiana (Avault, 1973).

These crayfish fisheries involve (1) baited traps, (2) no size limit, and (3) no bag limit or set season. In most instances, size determines marketability; only the larger crayfish are marketed. Availability is governed by water temperature and rate of growth. Thus availability is seasonal. Females carrying eggs are not readily harvested by the gear. As long as the method of harvest depends on the movement of crayfish, it (harvest) fails to affect reproductive stocks.

We patterned our harvest regime after existing fisheries, especially that for O. virilis in Wisconsin. In Wisconsin, crayfish are harvested with baited wire traps. There is no size limit. Most of the

Table 11. Cohort mean biomass ($\bar{B}^1$), cohort production (P^1), and cohort turnover ratio (TR^1) for crayfish populations in West Lost and North Twin lakes.

Lake and year	$\bar{B}^1$ kg/ha	P^1 kg/ha	TR^1
West Lost			
1966	18.8	108.5	5.77
1967	15.6	71.9	4.61
1968	18.8	105.5	5.61
1969	13.7	73.4	5.36
North Twin			
1966	14.3	75.0	5.24
1967	9.4	53.6	5.70
1968	9.5	54.2	5.70
1969	12.0	56.5	4.71

Table 12. Cohort production of age-0 male crayfish in West Lost and North Twin lakes.

Year	Cohort production in kg/ha	
	West Lost	North Twin
1966-67	28.64	26.57
1967-68	14.54	17.67
1968-69	33.17	21.52
1969-70	16.06	16.67
1970-71	9.57	5.27
1971-72	18.78	9.18
1972-73	12.52	8.44

trapping occurs after mid-July, is confined to shallow waters, and involves mainly third-year males larger than 45 mm in cephalothorax length. Since the growth rate was lower for our populations, we selected a carapace length of 30 mm as a size limit. We used wire traps as harvest gear. We selected a set number of traps (30) simply to standardize effort at 150 trap-days. This was also the reason for choosing 5 days as the length of the fishing season. We set no bag limit, since no existing fishery has such a limit. The study lakes are relatively small bodies of water. Hence, the decline in catch per unit of effort after 5 days of trapping made it uneconomical to fish much beyond the allotted time (Table 13).

Since females grow at a much slower rate than males and, in addition become unavailable to the gear during the season when deployed due to seasonal migration (Momot and Gowing, 1972), traps are selective for males.

Proper evaluation of our harvest strategy required that we consider the effect it had on both the target population and on the fishery itself. Our goal was to fish according to a maximum yield strategy in order to benefit both the population and the fishery. Presumably maximizing biological production in the population would benefit the fishery. As anticipated, the number and weight of crayfish harvested from the population stabilized (Tables 2, 14). The low yield in North Twin Lake in 1973 was caused by a lower efficiency in harvest rather than by a decline in population size (Tables 2, 14). According to the model employed, we fished at a sustained rate of yield. To test whether this is really the maximum sustained yield, we could have deliberately overfished. With the sustained yields, some of the anticipated biotic responses have not occurred. No dramatic change in age composition toward larger numbers of young animals was noted. In fact, age-I males were somewhat less abundant than before exploitation occurred. However, age-I females did increase. This may have been due to interaction between crayfish of the same age. Thus, the decrease in age-I males was compensated by the increase in age-I females (Table 4). This somewhat unexpected result has had another impact on the population. With the increase in age-I female crayfish, survival to age-II decreased,

Table 13. Catch per unit of effort (mean number of crayfish per trap) from West Lost and North Twin lakes from 1970 to 1973.

Lake and day	Number: Crayfish caught	Number: Traps	Mean catch per trap	Number: Crayfish caught	Number: Traps	Mean catch per trap
		1970			1971	
West Lost						
1	776	30	25.9	682	30	22.7
2	721	30	24.0	423	30	14.1
3	633	30	21.1	149	30	5.0
4	550	30	18.3	128	30	4.3
5	326	30	10.9	155	30	5.2
		1972			1973	
1	212	30	7.1	303	30	10.1
2	271	30	9.0	429	30	14.3
3	260	30	8.7	192	30	6.4
4	199	30	6.6	136	30	4.5
5	304	30	10.1	91	30	3.0
North Twin		1970			1971	
1	199	30	6.6	314	30	10.5
2	179	30	6.0	214	30	7.1
3	227	30	7.6	141	30	4.7
4	168	30	5.6	134	30	4.5
5	103	30	3.4	120	30	4.0
		1972			1973	
1	334	60	5.6	337	60	5.6
2	345	60	5.8	206	60	3.4
3	274	60	4.6	178	60	3.0
4	239	60	4.0	98	60	1.6
5	221	60	3.7	75	60	1.2

Table 14. Harvest in kilograms of crayfish from West Lost and North Twin lakes from 1970 to 1973.

Lake and year	Harvest (kg)		Total
	Male	Female	
West Lost			
1970	34.89	0.12	35.02
1971	15.17	0.90	16.07
1972	13.92	0.46	14.38
1973	12.30	0.10	12.40
North Twin			
1970	10.40	0.38	10.78
1971	9.76	0.28	10.04
1972	15.64	0.83	16.47
1973	9.38	0.52	9.90

as did mean fecundity caused by the crowding at the sublegal level (Table 7). As a result, egg production and eventually recruitment did not respond to exploitation as expected (Tables 5 and 8). Presumably this response might not have occurred had both sexes been available for harvest. At the same time, habitat quality decreased (Table 9). Thus, the decline in habitat quality no doubt equally contributed to the decreased recruitment in these populations. The decrease in recruitment had affected both the mean summer biomass and the annual production (Table 10). The decrease in production among males in West Lost was primarily among age-0, age-I, and age-II animals (Table 15). In North Twin Lake the greatest decrease was among age-0 crayfish. However, these decreases were already evident in 1970-1971 and affected primarily age groups not subject to harvest (Table 15). The decrease was caused by poor recruitment, not by excessive removal in the fishery. This conclusion was reinforced by examining cohort production (Table 16). The 1970, 1971, and 1972 cohorts were those produced since exploitation began, and they show a lower production value for age-0 and age-I males than for earlier cohorts. This was caused mainly by poor recruitment, since growth had not declined (Table 6) and since instantaneous growth rates have not changed (Table 17). In addition, no substantial trends or changes were noted for the instantaneous mortality rates (i) for these same age groups since exploitation (Table 18).

The fishery, by protecting females, had no direct effect on recruitment. The readjustment in population densities between males and females combined with environmental changes, caused decreases in fecundity and recruitment. Exploitation did not decrease production and harvest, but neither was there an increase in these parameters, as had been expected.

Our strategy produced a sustained yield to the fisherman following a large initial temporary yield. This classical development of the fishery agrees with the theory about yields obtained from initially unexploited stocks (Ricker, 1958).

Table 15. Annual production (kg) of crayfish by age group.

Lake, sex, age, and total	Production 1966-67	1967-68	1968-69	1969-70	1970-71	1971-72	1972-73
West Lost							
Male							
0	28.64	14.54	33.17	16.06	9.57	12.51	10.02
I	37.01	37.33	32.09	47.06	24.38	24.97	25.43
II	29.64	9.86	15.37	13.60	9.62	7.46	8.70
III	14.88	5.88	3.00	0.25	3.32	3.34	3.42
Total	110.17	67.36	83.65	76.97	46.89	48.28	47.57
Female							
0	32.01	14.94	22.24	17.91	8.83	12.26	10.17
I	32.68	30.36	18.93	28.54	27.58	40.03	15.72
II	10.95	5.66	6.44	2.45	1.65	4.64	4.52
III	1.60	3.34	1.71	1.48	1.00	2.11	1.37
Total	77.24	54.30	49.32	50.39	39.06	59.04	31.78
North Twin							
Male							
0	26.57	17.67	21.52	16.67	5.27	8.02	5.49
I	50.05	19.89	27.80	21.08	58.43	18.86	15.22
II	19.34	4.00	23.11	11.55	8.72	10.92	6.03
III	3.21	6.32	3.44	0.14	2.35	2.66	2.56
Total	99.17	47.88	75.87	49.44	44.77	40.46	29.30
Female							
0	23.76	17.70	22.65	15.58	5.11	7.41	6.23
I	30.69	42.21	18.38	20.28	32.25	26.18	19.82
II	9.39	5.12	6.69	5.25	3.93	6.75	6.97
III	0.49	0.16	2.04	0.23	1.17	2.23	4.16
Total	61.47	65.19	49.76	41.34	42.45	42.57	37.18

Table 16. Estimated cohort production (kg) of crayfish by age group from West Lost and North Twin lakes.

Lake, sex, age, and totals	Cohort production						
	1966	1967	1968	1969	1970	1971	1972
West Lost							
Male							
0	28.64	14.54	33.17	16.06	9.57	12.51	10.02
I	37.33	32.09	47.06	24.38	24.97	25.43	.....
II	15.37	13.60	9.62	7.46	8.70	.....	.....
III	0.25	3.23	3.34	3.42	.....	.....	.....
Total	81.59	63.46	93.19	51.32	.....	.....	.....
Female							
0	32.01	14.94	22.24	17.91	8.84	12.26	10.17
I	30.36	18.93	28.54	27.58	40.03	15.72	.....
II	6.44	2.45	1.65	4.64	4.52	.....	.....
III	1.48	1.00	2.11	1.37	.....	.....	.....
Total	70.29	37.32	54.54	51.50	.....	.....	.....
Grand total	151.88	100.68	147.73	102.82	.....	.....	.....
North Twin							
Male							
0	26.57	17.67	21.52	16.67	5.27	8.02	5.49
I	19.89	28.80	21.08	23.43	18.86	15.22	.....
II	23.11	11.55	8.73	10.92	6.03	.....	.....
III	0.14	2.35	2.66	2.56	.....	.....	.....
Total	69.71	59.37	53.99	58.58	.....	.....	.....
Female							
0	23.76	17.70	22.65	15.58	5.11	7.41	6.23
I	42.21	18.38	20.28	32.25	26.18	19.82	.....
II	6.69	5.25	3.93	6.75	6.97	.....	.....
III	0.23	1.17	2.23	4.16	.....	.....	.....
Total	72.89	42.50	49.09	58.74	.....	.....	.....
Grand total	142.60	101.87	103.08	107.32	.....	.....	.....

Table 17. Instantaneous growth rates (g) of crayfish from West Lost and North Twin lakes from 1966 to 1973.

Lake, sex, and age	Instantaneous growth rates						
	1966-67	1967-68	1968-69	1969-70	1970-71	1971-72	1972-73
West Lost							
Male							
0	2.22	2.57	2.22	2.22	1.62	2.22	2.11
I	2.56	2.31	2.38	2.34	2.34	2.86	2.41
II	0.60	0.53	0.67	0.48	0.58	0.57	0.71
III	0.55	0.66	0.46	0.46	0.45	0.41	0.58
Female							
0	2.22	2.22	2.22	2.22	1.52	2.22	2.03
I	2.22	2.14	2.12	2.03	2.10	2.78	1.99
II	0.54	0.49	0.45	0.35	0.47	0.36	0.30
III	0.35	0.48	0.48	0.68	0.36	0.37	0.41
North Twin							
Male							
0	2.72	2.34	2.45	2.22	1.86	2.20	2.22
I	2.23	1.89	2.18	1.83	2.29	2.78	2.25
II	0.45	0.22	0.90	0.63	0.85	0.77	0.50
III	0.31	0.40	0.67	0.56	0.48	0.62	0.28
Female							
0	2.52	2.22	2.34	2.13	1.86	2.16	2.22
I	1.91	1.81	2.00	1.83	2.19	2.52	2.21
II	0.40	0.45	0.50	0.58	0.53	0.51	0.51
III	0.56	0.52	0.54	0.68	0.33	0.48	0.36

Table 18. Instantaneous mortality rates (i) for crayfish in West Lost and North Twin lakes from 1966 to 1973.

Lake, sex, and age	Instantaneous mortality rates						
	1966-67	1967-68	1968-69	1969-70	1970-71	1971-72	1972-73
West Lost							
Male							
0	1.95	2.36	1.01	1.47	1.24	1.35	1.13
I	2.61	1.86	0.95	2.86	2.31	2.66	1.99
II	1.38	0.01	0.31	0.26	0.43	0.16	0.27
III	5.24	4.16	4.02	4.07	4.34	2.12	3.04
Female							
0	1.74	2.01	1.71	1.29	1.17	1.33	0.97
I	2.65	2.41	1.77	1.83	1.97	1.61	1.63
II	1.53	0.49	0.16	1.31	0.58	0.58	1.38
III	3.49	3.96	3.65	5.12	1.31	2.53	3.73
North Twin							
Male							
0	0.98	2.57	1.19	0.35	1.66	2.04	1.98
I	2.17	1.02	1.03	2.60	2.79	2.04	1.25
II	1.87	0.77	1.47	0.96	0.45	0.02	0.12
III	3.11	3.08	3.17	4.54	3.54	3.30	2.14
Female							
0	0.84	2.33	0.92	0.30	1.72	2.12	1.74
I	2.31	1.77	1.64	2.80	2.21	1.03	0.50
II	1.13	0.90	0.88	0.96	0.15	0.75	1.35
III	4.20	3.73	2.46	3.97	2.04	1.97	2.67

In Wisconsin, typical commercial yields averaged 7.2 to 7.5 crayfish per trap (Threinen, 1958). In West Lost Lake the initial catch per unit of effort exceeded the 7.2 mean but fell below this level by the fifth day of harvest. North Twin Lake provided a marginal crayfish fishery. At twice the effort the total catch increased, but the catch per unit of effort fell considerably below the 7.2 level. The Wisconsin lakes are considerably larger in area. One of the best fishery sites in Wisconsin was estimated to have produced 37.3 kg/ha. Our best yield was 24.9 kg/ha in West Lost in 1970. However, since 1970 the yield has averaged about 14.3 kg/ha. Low standing crops preclude an economically viable fishery in the Pigeon River Area lakes. At the intensity with which we fished, we cropped 25%-60% of the available biomass within the 5-day period. Many lakes have standing crops much greater than those found in our lakes (Gowing and Momot, 1974). Under intensive cultivation, yields approaching 500 kg/ha are not unusual, and wild crayfish stocks often exceed such yields (Broom, 1961; Langlois, 1936; Lydell, 1938).

The harvest of wild stocks of crayfish can be managed for maximum sustained yield. Present methods of harvest do not affect females, so our maximum-yield strategy affords maximum protection to the spawning stock. In this case, even if size limits did not protect females, their low susceptibility to traps would be more than adequate. In addition, the maximum biomass production in these lakes is achieved at age 1.5 and at a length of 30 mm (Table 6). With the age at entry into the fishery at 2.5 (Table 3), we are slightly underharvesting. The philosophical differences to approaching the maximum-yield problem rest on whether to maximize living tissue or minimize wastage due to natural mortality (Watt, 1968). In our crayfish populations, fortunately these options coalesce at about age 1.5. Intrinsic mechanisms keep production at about the same level each year. Our best strategy is to optimize living tissue, since this coincides with maximum reproductive strategy in our populations. This strategy is dictated by the short life span of crayfish.

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