POPULATION DYNAMICS OF AN EXPLOITED POPULATION OF **Orconectes virilis** IN NORTHWESTERN ONTARIO

by

George E. Morgan ©

Department of Biology
Lakehead University

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He gave a hollow laugh. `What does it matter? Science has achieved some wonderful things of course, but I'd rather be happy than right any day.'
`And are you?'
`No. That's where it all falls down of course.'
`Pity,' said Arthur with sympathy. `It sounded like quite a good lifestyle otherwise.'

Slartibartfast and
Arthur Dent
"Hitch Hiker's Guide
to the Galaxy"

`Well, I mean <u>yes</u> idealism, <u>yes</u> the dignity of pure research, <u>yes</u> the pursuit of truth in all its forms, but there comes a point I'm afraid where you begin to suspect that if there's any <u>real</u> truth, it's that the entire multi-dimensional infinity of the Universe is almost certainly being run by a bunch of maniacs. And if it comes to a choice between spending yet another ten million years finding that out, and on the other hand just taking the money and running, then I for one could do with the exercise,' said Frankie.

Frankie the mouse
"Hitch Hiker's Guide
to the Galaxy"

This thesis is dedicated to my parents, Dr. & Mrs. Roger E. Morgan, for their emotional and financial support for all these years.

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I would like to thank my fellow graduate students for inspiration when it was needed, advice when it was required and excuses to drink when I'd had enough bull sh*t. My sincere and heartfelt thanks to Al Dextrase & Helen Ball, Tim Keenan & Rebecca Counts (and Caitlin), Shawn & Marg Stevenson (and Gaelan), Lud Krysl & Bev Ritchie, Mike Fruetel, Kevin & Sue Trimble, Arnie & Elaine Laine (and ?), Brian Wisenden, Sandra McIver, Dave Reid & Mayda Palcic, Larry Schincariol and Jeff & Sabine Maxwell. Without your help and support I would probably be break-dancing with Al in front of the Hoito Restaurant for a living.

I thank Dr. Walter T. Momot for giving me the chance to pursue my own ideas, whether they were right, wrong or just different. My work would not have been possible without his encouragement (or indifference?) to manipulate his excellent long-term data set. Please remember Walter, TEMPERATURE EFFECTS CAN NOT BE SUBSTANTIATED.

I cannot thank my wife Leslie enough for her support over these last years. Her love, persistence and endurance through the trials and tribulations, the good and bad times, and Lakehead University have made the difference.

Computer processing, graphics preparation and printing was generously provided by Dr. Peter F. Lee (and his Riceroni's) and Al Smith. Typing of the tables was done by Ms. Kris Delorey. Without your unselfish support this thesis would probably be on clay tablets (due to fiscal restraints).

If I have forgotten to thank anyone, please feel free to write your name and contribution in the spaces provided below:

Name	Assistance Provided
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(5)	

PREFACE

This thesis is written as five separate chapters related to individual population parameters: (1) reproduction dynamics, (2) growth responses, (3) alteration of mortality patterns, (4) harvest assessment and (5) population regulation. The individual chapters are manuscripts that are presently being submitted for publication in various journals. I have not attempted to join these individual sections into an overall discussion, but do provide a unified abstract and summary. Each manuscript contains an abstract, introduction, methods, results and discussion section. All necessary information required for evaluation of my research is self-contained within each chapter. I am solely responsible for the results and the biological interpretations that were made. All analysis and corresponding results are mine, but, co-authorship with Dr. Walter T. Momot requires that the impersonal, nominative _we_ be used.

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ABSTRACT

Exploitation of northern stocks of the crayfish **Orconectes virilis** (Hagen) produced significant alterations in several population parameters. High fishing efforts increased per capita fecundity, young-of-year (YOY) production, and age- and sex-specific growth, and altered mortality patterns. Climatic variation, measured as arbitrarily defined weather variables, did not influence life history parameters in the exploited population. However, short-term temperature fluctuations affected YOY production and future reproductive potential in the control lake. The control population in Shallow Lake exhibited strong density dependence in regulating both mortality and growth rates of pre-recruit age classes. Behavioural dominance by maturing males (age I-to-age II) effectively controlled juvenile life history parameters , i.e., egg-to-YOY and YOY-to-age I mortality and growth. As a result a dynamic oscillatory relationship existed between annual age I-to-age II male growth and female year-class strength, which in turn correlated with cohort egg production. Exploitation of Dock Lake's population broke down this process so that year-class strength directly correlated with annual growth but cohort egg production varied independently. The amount harvested, using passive fishing gear, proportionately increased with increases in nominal effort. However interactions between sampling intensity, duration of harvest and behavioural responses resulted in a upper limit to the percent of the exploitable stock that that could be removed by this fishery. Alteration of life history parameters contributed to population resilience and stability as fishing pressure increased.

FECUNDITY & PRODUCTION OF YOUNG

Morgan, G.E. & W.T. Momot. 1987. Reproductive dynamics of the crayfish Orconectes virilis in two northwestern Ontario lakes. In preparation.

ABSTRACT

Female crayfish in Dock Lake responded to exploitation by increasing reproductive capability, measured as changes in age-specific pleopod egg counts, and young-of-year (YOY) production. In contrast the unfished population in Shallow Lake had lower fecundity as well as significantly lower YOY production. Mature female fecundity (age I+) increased over the last ten years in both lakes. However since 1981 Dock Lake females have produced more eggs per female. This is the result of increased growth potential induced by exploitation. In Dock Lake, mature female fecundity was related to natural mortality during the fall/winter period, while in Shallow Lake fecundity was related to annual growth. First time spawners (age 0+) in both lakes produced an average 108 eggs per female. Although per capita fecundity differed, annual total egg production was similar between lakes. YOY production in Dock Lake increased to a threshold where available habitat limited recruitment (i.e., constant YOY production). Variability in Shallow Lake YOY survival rates was related to spring temperatures. Apparently the Dock Lake growth response together with an environmentally forced time lag in Shallow Lake produced the following results: (1) a differential egg-to-YOY survival between lakes, (2) a two year lag in Shallow Lake mature female fecundity, (3) a reduction in Shallow Lake egg quality, and (4) a reduction in Shallow Lake female weight growth potential. Possible indices for detection of fecundity failures involve: relationships between egg weight and size of female, and differences in egg production per unit length between first time spawners and mature females. Harvesting 30-40% of the exploitable female stock increased mature female fecundity and YOY production. The importance of measuring reproductive responses for assessment and management of benthic crustaceans are discussed.

INTRODUCTION

Since 1976 extensive data has been collected on the crayfish **Orconectes virilis** (Hagen) from two small marl lakes in northwestern Ontario. Our objective was to over-exploit the crayfish population in Dock Lake so as to compare it's responses to an unexploited population in nearby Shallow Lake. In this study we therefore investigated possible relationships between the female population, fecundity and YOY production. In particular could we: (1) detect any fecundity response as fishing pressure increased in Dock Lake, (2) predict whether fecundity could be related to biotic or abiotic factors in either lake and (3) detect whether changes in YOY production could be attributed to changes in fishing effort.

The only other study of the possible responses of crayfish populations to exploitation is that of Momot and Gowing (1977a, b and c) in three oligotrophic Michigan lakes. In that study selective male exploitation resulted in a negative feedback causing a density-dependent adjustment between female age I and age II survival rates and fecundity. In addition survival of young-of-year (YOY) decreased as a result of a decline in nursery habitat (Momot and Gowing 1977c). This reduced reproductive potential (i.e., age-specific fecundity and YOY production) which in turn decreased recruitment to the exploitable stock. Momot and Gowing (1977a) concluded that "the major response in the production process is probably through survivorship and egg production rather than growth."

Other researchers commonly relate fecundity to body morphometrics (Brown and Bowler 1977; Shimizu and Goldman 1981;

Eng and Daniels 1982), disparity between ovarian and pleopod egg counts (Momot 1967; Prins 1968; Payne 1971; McGriff 1983), relationship to abiotic factors (Aiken 1969), occurrence of repeat spawning (Morrissy 1975) or deferred reproduction (Brewis and Bowler 1985), comparisons between species (Abrahamsson 1971; Hamr and Berrill 1985) and clinal variations within a species (Abrahamsson 1972). However quantitative information on yearly variation, regulation of egg production and the effect of exploitation on fecundity is insufficient for management of crayfish populations. More important is the relationship between fecundity and YOY recruitment in an exploited population. There are no published accounts which deal fully with the effects of fecundity variation on crayfish recruitment.

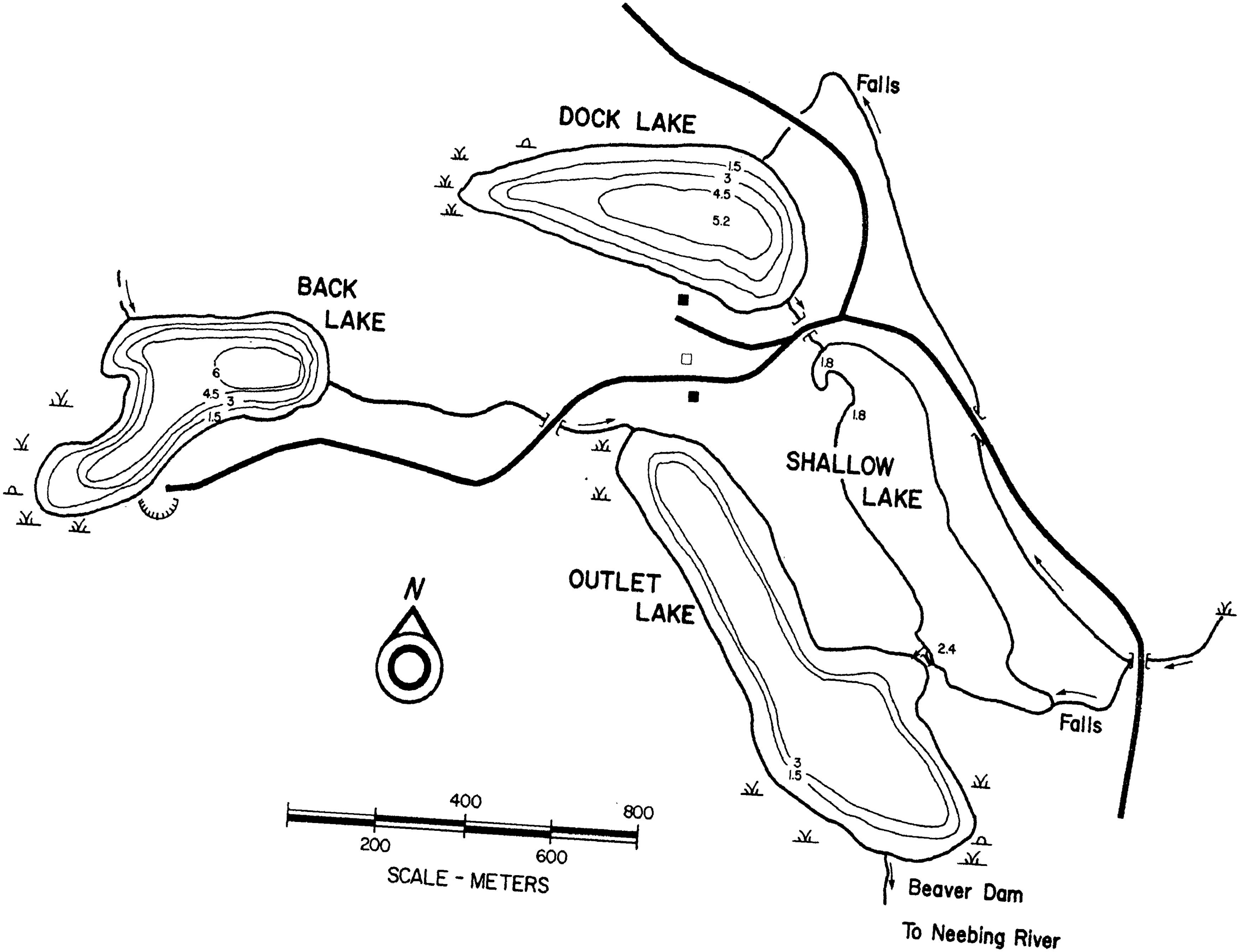
STUDY AREA AND METHODS

Study Area

The two small marl study lakes, Dock and Shallow, are situated within the municipal boundary of Thunder Bay, Ontario, Canada, 10.5 km west of Lake Superior (48° 28'N 89° 28'W). The local topography is composed of rounded ridges of granitic bedrock with valley flats of deeper soils (Hills 1959). Grey wooded or brown podsol soils are common on well-drained areas while valley bottoms are usually peat. Boreal mixedwood forest and associated understory shrubs extend to the shoreline of both lakes.

Thunder Bay has a modified continental climate due to the warming affect of nearby Lake Superior (Anon. 1973). The average

Figure 1. Map of Powell's Lakes, McIntyre Township, Thunder Bay, Ontario. Depth contours are given in metres.


DOCK LAKE
1.5
3
4.5
5.2
Falls
BACK LAKE
6
4.5
3
1.5
1.8
1.8
SHALLOW LAKE
OUTLET LAKE
2.4
Falls
3
1.5
N
400
800
200
600
SCALE - METERS
Beaver Dam
To Neebing River

annual mean temperature is 2.3 ^{o}C with a maximum annual mean of 8.3 ^{o}C and a minimum annual mean of -3.7 ^{o}C (Anon. 1985). Mean summer (May to September) temperature is 13.6 ^{o}C. Prevailing winds from the east during the late spring and early summer have a marked cooling effect on local temperatures. Normal yearly precipitation is 527.3 mm of rain and 213.0 mm of snow (Anon. 1985). Seventy-five percent of the rain occurs during the summer months (May to September precipitation = 393.4 mm).

Dock Lake has a surface area of 1.2 ha with a mean depth of 2.4 m and a maximum depth of 5.2 m (Momot 1978). Shallow Lake is 1.6 ha in size with a mean depth of 2.2 m and a maximum depth of 2.4 m at the outlet (Fig. 1). Shallow Lake remains homothermous while Dock Lake thermally stratifies during the summer months. Both lakes are in an early senescent stage of eutrophy, having high values for nutrients, dissolved solids, conductivity and alkalinity (Momot 1978). The bottom substrate mixtures of sand and gravel are overlain by marl of varying thickness. The aquatic macrophyte vegetation is quite dense in both lakes reaching to a depth of 3 m in Dock Lake and to bottom in Shallow Lake. Large monospecific stands cover extensive areas in Dock and Shallow Lake with beds of the macroalgae muskgrass, Chara vulgaris L., defining much of the physiognomy of the littoral zone <1.5 m. The limited ichthyofauna of Dock and Shallow Lake is dominated by minnows (Family Cyprinidae) and stunted white suckers (Catostomus commersoni (Lacepede)). The study was initiated in May 1976 and is ongoing; results up to September 1985 are examined and summarized.

General Methods and Sampling Design

The general methods and sampling design of the research program are described in this manuscript. Subsequent papers will deal with detailed analysis of field studies and population ecology.

Annual sampling commenced in mid-May to early June when the water sufficiently warmed (greater than 10^{o} C) to cause sexually mature female crayfish to extrude eggs (Aiken 1969). Some parturient females were collected by hand from artificial shelters (small terra cotta pots sectioned longitudinally) placed on favourable substrates along the shorelines of both lakes. Other egg-bearing females were collected at random from under rocks along the shoreline. In Shallow Lake, egg-carrying females were also caught in minnow traps. Age-specific fecundity, measured as pleopod egg counts, when combined with spring female density estimates were used to calculate yearly population reproductive output (i.e., by summing the respective contribution of each mature age-groups total egg production). Brood wet weight and somatic wet weight of the females were measured to the nearest 0.001 gram using a digital balance for the spring 1985 fecundity sample in Dock and Shallow Lake.

Adults and yearlings were captured with modified minnow traps (44.5 cm long X 23 cm at largest diameter with inwardly directed funnel entrance holes expanded to 3-5 cm diameter at each end, mesh of 6.25 mm and weighing approximately 0.7 kg). These traps were baited with 40-60 gm of frozen fish. The most commonly used bait was American Smelt (Osmerus mordax (Mitchill)). These crayfish, given a recognizable mark by excision of the pleurae, were returned to the lake (Momot 1967). The pleural clips were coded for each year and population sample. Young-of-year (YOY) were collected annually at approximately the same time interval by hand nets and marked by partial excision of a uropod. Population densities in these closed systems were estimated using the Schumacher-Eschmeyer formula (Ricker 1975). In spring only sexually mature female densities were estimated. The number of YOY, yearlings, adult males and females were estimated in the summer from mid-July to early August during the intermoult period.

All captured yearling, adult and approximately 100 to 400 YOY were measured to the nearest 0.5 mm from the tip of the rostrum to the posteriomedial edge of the carapace using vernier calipers. Length refers to carapace length (CL) in mm. Age composition was analysed from size frequency polygons and verified from modal progressions of previously marked animals of known age (Cassie 1954; Momot 1967). Growth rates were determined by following size modes that correspond to age-classes through plots of size distribution for several sequential years. Seasonal length-wet weight relationships of the population in Dock Lake were computed from empirical data collected in 1976 (Momot unpublished data), and during the harvests of 1984 and 1985.

We calculated a maturity schedule for both males and females from a size-stratified sample collected during the 1985 harvest. Maturity in 229 males (22 to 47 mm CL) and 195 females (21 to 43 mm CL) was determined by examination of both external sex characteristics and dissection of testes and ovaries. The cyclic dimorphism of males between the non-reproductive form II and the reproductive form I was used to determine sexual maturity. Form II males were also considered mature if the vas deferens was visibly thickened or contained sperm (McGriff 1983). This avoided changes in maturity caused by the timing of the sample in relation to the moult from form II to form I (Lorman 1980). Females were considered mature if the ovaries contained developing oocytes or if the cement gland development was stage 2 or greater (Stephens 1952). The mean size at onset of sexual maturity was determined by the methods of Wenner et al. (1974) and by fitting a logistic function to the size-specific maturity data (i.e., size versus maturity ogive) .

Age- and sex-specific survival and mortality rates were calculated from sequential population estimates. Exploitation rates were estimated from the recapture of marked individuals during the harvest (Ricker 1975). Also Petersen estimates from the mark-recapture studies provided independent population estimates which corroborated the Schumacher-Eschmeyer technique (Momot unpublished data; Ricker 1975).

The harvest of the crayfish population in Dock Lake increased from an initial 150 trap-days (30 traps for 5 days) in 1977 to 1350 trap-days in 1978 (150 traps for 9 days). A trap-day consists of a single minnow trap fished 24 hours. From 1979 until 1981 the effort increased to 2600 trap-days (200 traps for 13 days). Effort, or nominal effort, is the number of trap-days during the harvest. Again in 1982 the effort further increased to 4000 trap-days (200 traps for 20 days). This level was maintained for 1983 and 1984. However in 1984 the fishing power changed to

Table 1. Average carapace length, fecundity and eggs per mm of carapace length for Shallow Lake yearling and mature females 1976 to 1985.

TABLE 1. Average carapace length, fecundity and eggs per mm of carapace length for Shallow Lake yearling and mature females 1976 to 1985.

Year	Yearling Females Carapace Length (mm)	Pleopod Eggs	Eggs Per mm	n	Mature Females Carapace Length (mm)	Pleopod Eggs	Eggs Per mm	n	Total Annual Fecundity	n
1976	23.0	14.0	0.6	1	31.1 ± 0.8	99.8 ± 24.7	3.1 ± 0.7	21	95.9 ± 23.9	22
1977	26.0 ± 0.6[1]	121.5 ± 44.3	4.6 ± 1.6	4	33.3 ± 0.9	132.1 ± 22.2	4.0 ± 0.7	19	130.3 ± 19.5	23
1978	29.0 ± 0.2	132.2 ± 10.9	4.6 ± 0.4	68	33.3 ± 0.4	199.8 ± 24.1	6.0 ± 0.7	18	148.0 ± 10.3	86
1979	26.4 ± 0.3	77.0 ± 12.4	2.9 ± 0.5	26	31.9 ± 0.6	172.1 ± 29.1	5.2 ± 0.8	12	107.0 ± 14.3	38
1980	27.7 ± 0.3	86.0 ± 9.9	3.1 ± 0.3	49	34.1 ± 0.5	92.1 ± 27.5	2.7 ± 0.8	10	87.0 ± 9.4	59
1981	28.6 ± 0.3	92.9 ± 18.5	3.2 ± 0.6	16	33.3 ± 0.4	144.7 ± 19.9	4.3 ± 19.9	35	128.5 ± 15.1	51
1982	28.7 ± 0.3	140.0 ± 11.8	4.9 ± 0.4	24	33.2 ± 0.2	201.3 ± 11.5	6.0 ± 0.3	59	183.6 ± 9.3	83
1983	26.0 ± 0.0	95.5 ± 30.5	3.7 ± 1.2	2	32.4 ± 0.3	172.8 ± 10.3	5.3 ± 0.3	63	170.4 ± 10.1	65
1984	25.6 ± 0.4	74.2 ± 17.4	2.9 ± 0.7	9	31.5 ± 0.4	150.8 ± 9.0	4.8 ± 0.3	46	138.3 ± 8.9	55
1985	28.4 ± 0.2	74.0 ± 7.9	2.6 ± 0.3	56	33.3 ± 0.3	108.0 ± 12.5	3.2 ± 0.4	63	92.0 ± 7.7	119
Total	28.1 ± 0.1	100.8 ± 4.8 (108.3 ± 5.6)[2]	3.5 ± 0.2	255	32.7 ± 0.1	152.5 ± 5.3	4.6 ± 0.2	346	130.5 ± 3.8	601

---

[1] Mean ± standard error

[2] 1976 - 1984 mean ± 1 standard error

Table 2. Average carapace length, fecundity and eggs per mm of carapace length for Dock Lake yearling and mature females 1976 to 1985.

TABLE 2. Average carapace length, fecundity and eggs per mm of carapace length for Dock Lake yearling and mature females 1976 - 1985.

Year	Yearling Females				Mature Females					
	Carapace Length (mm)	Pleopod Eggs	Eggs Per mm	n	Carapace Length (mm)	Pleopod Eggs	Eggs Per mm	n	Total Annual Fecundity	n
1976	27.9 ± 0.3[1]	110.4 ± 19.6	3.9 ± 0.7	16	32.8 ± 0.5	169.4 ± 17.5	4.2 ± 0.5	27	147.5 ± 13.8	43
1977	27.5 ± 0.3	91.1 ± 16.8	3.3 ± 0.6	17	33.0 ± 0.7	104.4 ± 25.1	3.2 ± 0.7	19	98.1 ± 15.3	36
1978	26.8 ± 0.3	116.0 ± 12.1	4.3 ± 0.4	22	32.0 ± 0.4	178.0 ± 17.4	5.6 ± 0.5	27	150.2 ± 11.8	49
1979	25.6 ± 0.3	75.0 ± 8.4	2.9 ± 0.3	26	30.9 ± 0.2	148.3 ± 7.1	4.8 ± 0.2	66	127.6 ± 6.6	92
1980	27.0 ± 0.2	97.1 ± 8.9	3.6 ± 0.3	45	32.3 ± 0.8	108.7 ± 27.5	3.3 ± 0.8	14	99.8 ± 9.3	59
1981	28.8 ± 0.2	154.4 ± 13.1	5.3 ± 0.4	25	32.1 ± 0.3	203.2 ± 19.4	6.3 ± 0.6	22	177.2 ± 11.9	47
1982	28.4 ± 0.3	111.2 ± 19.3	3.9 ± 0.7	11	32.6 ± 0.3	224.3 ± 11.2	6.9 ± 0.3	48	203.2 ± 11.3	59
1983	27.7 ± 0.4	117.6 ± 14.2	4.2 ± 0.5	24	32.7 ± 0.3	193.8 ± 10.1	5.9 ± 0.3	66	173.5 ± 9.0	90
1984	27.2 ± 0.2	112.2 ± 8.6	4.1 ± 0.3	38	33.3 ± 0.4	167.0 ± 12.1	5.0 ± 0.3	60	145.7 ± 8.5	98
1985	25.7 ± 0.3	104.4 ± 9.1	4.0 ± 0.3	29	31.2 ± 0.3	167.5 ± 7.6	5.3 ± 0.2	91	152.0 ± 6.7	120
Total	27.1 ± 0.1	108.1 ± 3.9	4.0 ± 0.1	253	32.1 ± 0.1	172.6 ± 4.1	5.4 ± 0.1	440	149.1 ± 3.2	693

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[1] Mean ± 1 standard error

250 traps without a change in the fishing effort (250 traps for 16 days). Fishing power is defined as the number of traps-per-unit-area. Beginning in 1985 the fishing effort was increased once more to 6000 trap-days (200 traps for 30 days). Harvesting began in late July, after completion of the summer population estimates, and was finished by the end of August.

Yearly meteorological records were obtained from the Thunder Bay Airport (48° 22′ N 89° 19′ W) to calculate intensity and frequency of heat input and precipitation during the sampling period. Because egg extrusion occurs in mid-May and the eggs begin to hatch by late May, annual weather variations for this month could influence reproductive success and YOY production. Thus weather parameters and indices were arbitrarily defined from the May climatological data time series. Growing-degree-days (GDD) was used as a measure of total accumulated heat. The number of days with daily mean temperature above the base temperature (for calculation of GDD) was used as a measure of the frequency of heat input.

RESULTS

Total annual fecundity between the exploited and control lake populations was compared with paired t-tests (Momot unpublished data). Only 1976 ($P<0.05$), 1981 ($P<0.015$) and 1985 ($P<0.001$) showed significant differences (Tables 1 and 2). However the spring population of egg producing females is composed of two units: (1) mature females - predominantly age I+ and a few age II+, all of these individuals are sexually mature

Figure 2. Time series of mature female fecundity in Dock Lake (exploited) and Shallow Lake (control) 1976 to 1985.

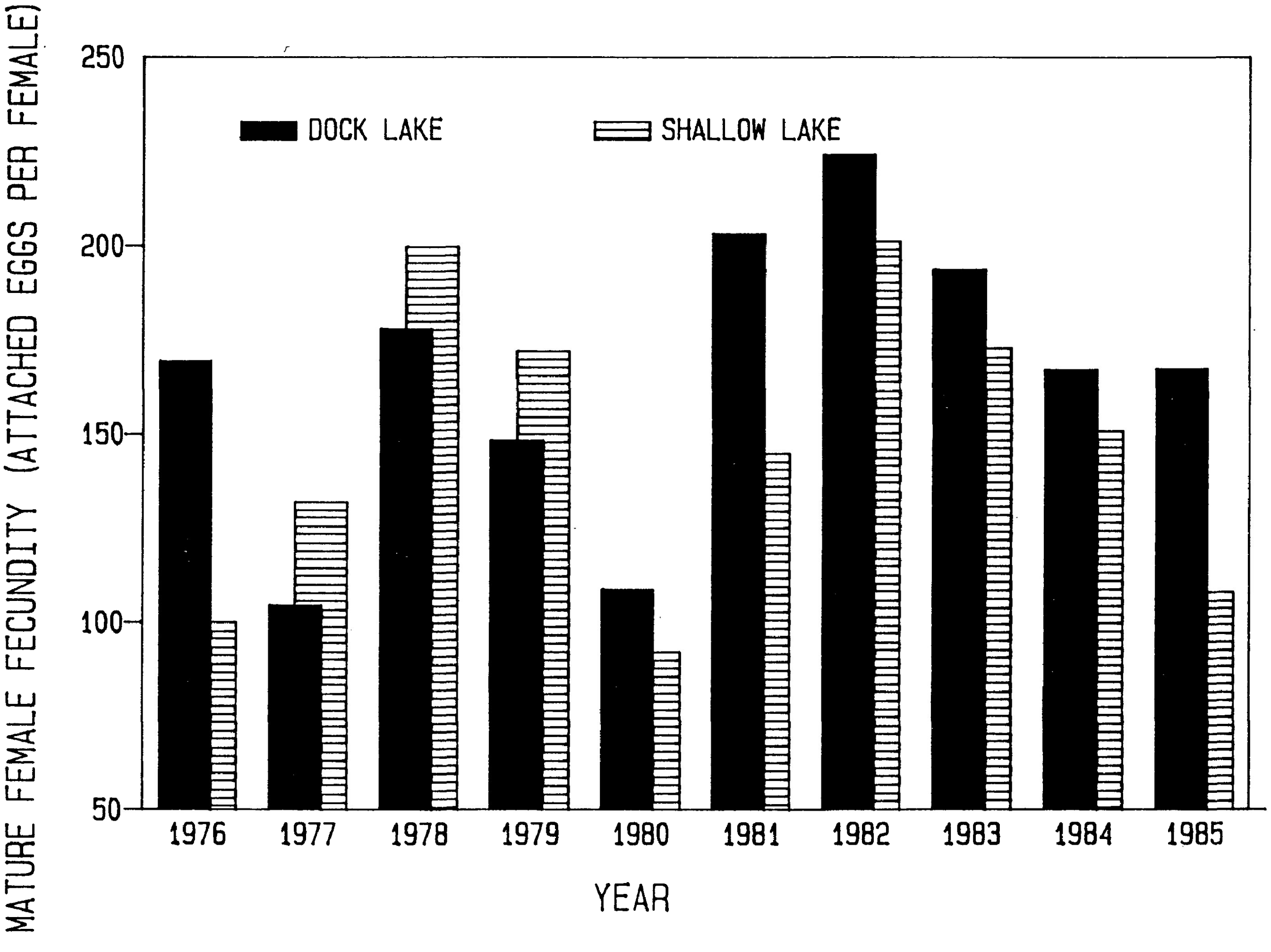
MATURE FEMALE FECUNDITY (ATTACHED EGGS PER FEMALE)
250
200
150
100
50
DOCK LAKE
SHALLOW LAKE
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

Table 3. Comparison between Dock and Shallow Lake yearling fecundity, mature female size and mature female fecundity by year intervals (1976-1980, 1981-1984 and 1985).

TABLE 3. Comparison between Dock and Shallow Lake yearling fecundity, mature female size and mature female fecundity by year intervals (1976-1980, 1981-1984 and 1985).

	Shallow Lake			Dock Lake		
Year Interval	Yearling Fecundity	Mature Female Size (mm)	Mature Female Fecundity	Yearling Fecundity	Mature Female Size (mm)	Mature Female Fecundity
1976 - 1980	107.0 ± 6.8[1]	32.6 ± 0.3	139.8 ± 12.0	96.7 ± 5.4	31.8 ± 0.2	148.2 ± 6.8
	(148)	(80)	(80)	(126)	(153)	(153)
1981 - 1984	111.9 ± 9.3	32.6 ± 0.2	171.3 ± 6.2	124.2 ± 6.4	32.8 ± 0.2	194.1 ± 6.3
	(51)	(203)	(203)	(98)	(196)	(196)
1985	74.0 ± 7.9	33.3 ± 0.3	108.0 ± 12.5	103.4 ± 9.1	31.2 ± 0.3	167.5 ± 7.6
	(56)	(63)	(63)	(29)	(91)	(91)

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[1] Mean ± 1 standard error (sample size)

(primiparous or multiparous), and (2) yearlings - age 0+, consisting of both sexually mature first time spawners (primiparous) and barren individuals (nulliparous). Population fecundity was separated into these naturally occurring groups for analysis and females will hereafter be classified as such.

Mature Female Fecundity

An interesting time trend is seen in mature female annual fecundity (Tables 1 and 2; Fig. 2). While mature females of Shallow Lake were generally more fecund up until 1980, Dock Lake females became more fecund after 1981. Analysis of variance (ANOVA) with a posteriori analysis of significant differences by the Scheffe method, alpha level = 0.05, revealed Dock and Shallow Lake mature female fecundity could be pooled within three yearly intervals, 1976-80, 1981-84 and 1985 (Dock Lake: $P<0.001$; Shallow Lake: $P<0.0001$). Both Dock and Shallow Lake mature female fecundity significantly increased between the 1976-80 and 1981-84 periods (Dock Lake: $P<0.001$; Shallow Lake: $P<0.03$) (Table 3). However no difference between Dock and Shallow Lake mature female fecundity occurred within the 1976-80 period ($P=0.55$). Beginning in 1981-84 mature female fecundity in the lakes significantly differed ($P<0.02$) with fecundity in Dock Lake increasing more so than in Shallow Lake.

The fecundity of Shallow Lake mature females significantly decreased in 1985 compared to 1981-84 ($P<0.001$) to a level approximating 1976-80 ($P=0.07$) (Table 3). In Dock Lake the females showed the same trends (1985 & 1981-84: $P<0.009$; 1985 & 1976-80: $P=0.07$). Though 1985 mature female fecundity decreased

Table 4. Comparison between Dock and Shallow Lake yearling and mature female eggs per mm by year intervals (1976-1980, 1981-1984 and 1985).

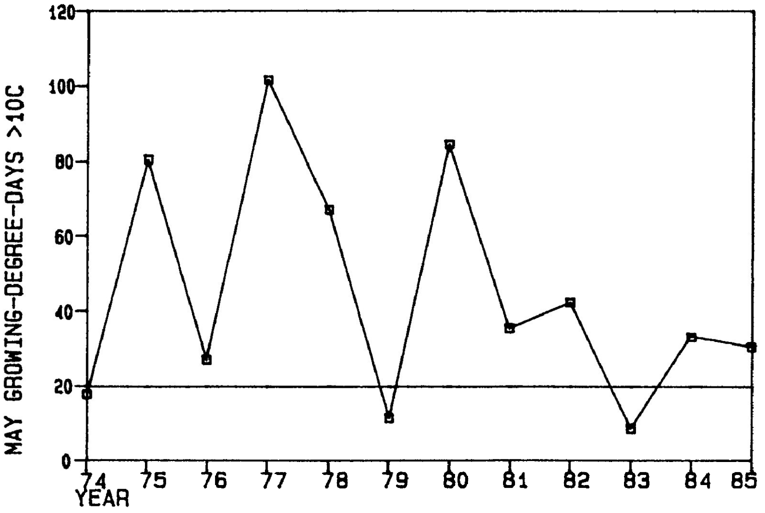
TABLE 4. Comparison between Dock and Shallow Lake yearling and mature female eggs per mm by year intervals (1976-1980, 1981-1984, and 1985).

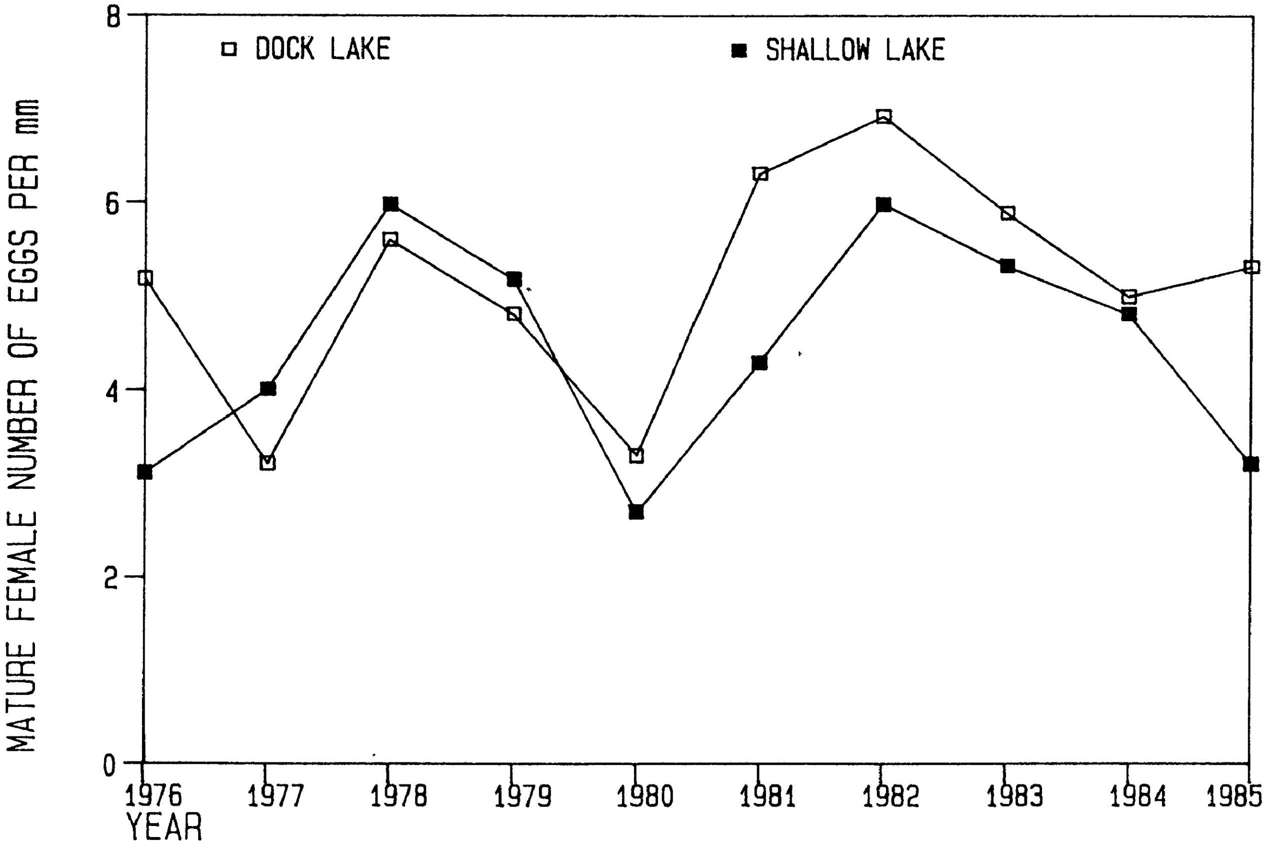
Shallow Lake		Dock Lake	
Year Interval	Eggs.mm^{-1}	Year Interval	Eggs.mm^{-1}
	Mature Females		
1976 - 1980	4.3 ± 0.4 (80)[1]	1976 - 1980	4.7 ± 0.2 (153)
1981 - 1984	5.2 ± 0.2 (203)	1981 - 1985	5.7 ± 0.1 (287)
1985	3.2 ± 0.4 (63)	1985	5.3 ± 0.2 (91)
	Yearling Females		
1976 - 1984	3.8 ± 0.2 (199)	1976 - 1985	4.0 ± 0.1 (253)
1985	2.6 ± 0.3 (56)	1985	4.0 ± 0.3 (29)

---

[1] Mean ± standard error (sample size)

Figure 3. Time series of mature female fecundity (eggs per mm of carapace length) in Dock Lake (exploited) and Shallow Lake (control) 1976 to 1985. Also time trend of number of growing-degree-days >10oC for the month of May (inset).


120
100
80
60
40
20
0
MAY GROWING-DEGREE-DAYS >10C
74
75
76
77
78
79
80
81
82
83
84
85
YEAR


8
6
4
2
0
□ DOCK LAKE
■ SHALLOW LAKE
MATURE FEMALE NUMBER OF EGGS PER mm
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

in both lakes this decrease was even greater in Shallow Lake ($P<0.001$; Table 3).

There was no difference between carapace lengths of mature females in Shallow Lake (Table 1). However Dock Lake females were larger in 1984 than in 1979 or 1985 (ANOVA: $P<0.0001$) (Table 2). For consistency, the female size analysis was conducted with the same time intervals. In Dock Lake during 1981-84 females were significantly larger than in either 1976-80 ($P<0.001$) or in 1985 ($P<0.001$) (Table 3). Also the 1985 Dock Lake females were significantly smaller than in 1976-80 ($P<0.001$). There was no difference between the same groups in Shallow Lake. More important is the within time interval comparisons. Mature Shallow Lake females during 1976-80 were significantly larger in size than those in Dock Lake ($P<0.05$). During 1981-84, the size of mature females did not significantly differ between lakes ($P=0.43$). This implies that Dock Lake mature females were larger in 1981-84 compared to 1976-80. In 1985, Shallow Lake females were significantly larger than those in Dock Lake ($P<0.001$).

The effect of varying female size on fecundity was analysed by estimating the number of eggs per millimetre of carapace length (eggs.mm^{-1}) (Tables 1, 2 and 4; Fig. 3). The numbers of eggs.mm^{-1} could be grouped into three intervals: 1976-80, 1981-84 and 1985 in Shallow Lake (ANOVA: $P<0.0001$). In contrast Dock Lake females were grouped into two time intervals: 1976-80 and 1981-85 (ANOVA: $P<0.0001$). Dock Lake females produced more eggs.mm^{-1} in 1981-85 than in 1976-80 ($P<0.001$). Shallow Lake females also produced more eggs.mm^{-1} in 1981-84 than in 1976-80 ($P<0.02$) but less in 1985 (1976-80: $P<0.04$; 1981-84: $P<0.001$). During 1976-80 females in both lakes produced on average the same number of $eggs.mm^{-1}$ (P=0.32). Dock Lake females produced more $eggs.mm^{-1}$ in 1981-85 than females in Shallow Lake in either 1981-84 (P<0.03) or in 1985 (P<0.001).

Yearling Females

In yearlings, fecundity varied little within either lake (Tables 1 and 2). The 1981 yearlings in Dock Lake were more fecund than those in 1979 (ANOVA; P<0.002). In Shallow Lake the 1978 yearlings were more fecund than those in 1985 (ANOVA: P<0.0001). However the small sample sizes make these differences statistically and biologically questionable (Table 3).

As well yearling female size tremendously varied. In Dock Lake 1981 yearlings were larger than those in: 1978, 1979, 1980, 1984 and 1985 while 1979 and 1985 females were smaller than those in: 1976, 1982, 1983 and 1984 (ANOVA: P<0.0001). In Shallow Lake 1979 and 1984 females were smaller than those in 1978, 1982 and 1985 (ANOVA: P<0.0001).

Hence we analysed the effect of size variability on the yearling fecundity by using $eggs.mm^{-1}$ of carapace length (Tables 1,2 and 4). Overall yearling females produce on average the same number of $egg.mm^{-1}$ in both Dock and Shallow Lake. No difference was noted between any years in Dock Lake. However Shallow Lake 1985 yearlings produced fewer $eggs.mm^{-1}$ than those in 1978 (ANOVA: P<0.0003). Shallow Lake yearlings were divided into two time periods, 1976-84 and 1985. Dock Lake yearling $eggs.mm^{-1}$ did not significantly differ from those in Shallow Lake during 1976-

Table 5. Relationship between carapace length and fecundity (pleopod egg counts) of Dock and Shallow Lake females by year (1976-1985) and year intervals (1976-1980, 1981-1984 and 1985).

TABLE 5. Relationship between carapace length and fecundity (pleopod egg counts) of Dock and Shallow Lake females by year (1976-1985) and year intervals (1976-1980, 1981-1984 and 1985).

Year	Shallow Lake					Dock Lake				
	Slope[1] (b)	Intercept (a)	r	R^2	n	Slope (b)	Intercept (a)	r	R^2	n
1976	9.39	-192.63	0.33	0.11	22	6.77	-62.14	0.24	0.06	43
1977	0.66	108.96	0.03	0.001	23	1.53	51.48	0.06	0.004	36
1978	12.95***	-239.54	0.35	0.12	86	6.98*	-56.74	0.27	0.07	49
1979	19.61***	-445.13	0.68	0.46	38	9.04***	-138.22	0.43	0.19	92
1980	3.06	- 1.17	0.13	0.02	59	4.22	- 19.31	0.18	0.03	59
1976 - 1980	8.71***	-139.45	0.31	0.10	228	6.48***	- 66.68	0.27	0.07	279
1981	10.53*	-207.18	0.29	0.08	51	11.00*	-156.85	0.29	0.08	47
1982	12.58***	-217.41	0.40	0.16	83	17.26***	-345.78	0.50	0.25	59
1983	14.12***	-284.35	0.51	0.26	65	12.41***	-215.99	0.45	0.20	90
1984	7.93***	-104.36	0.43	0.18	55	9.52***	-148.49	0.46	0.21	98
1981 - 1984	11.51***	-205.16	0.40	0.16	254	11.68***	-193.21	0.44	0.19	294
1985	9.10***	-190.20	0.35	0.12	119	11.14***	-180.63	0.53	0.28	120

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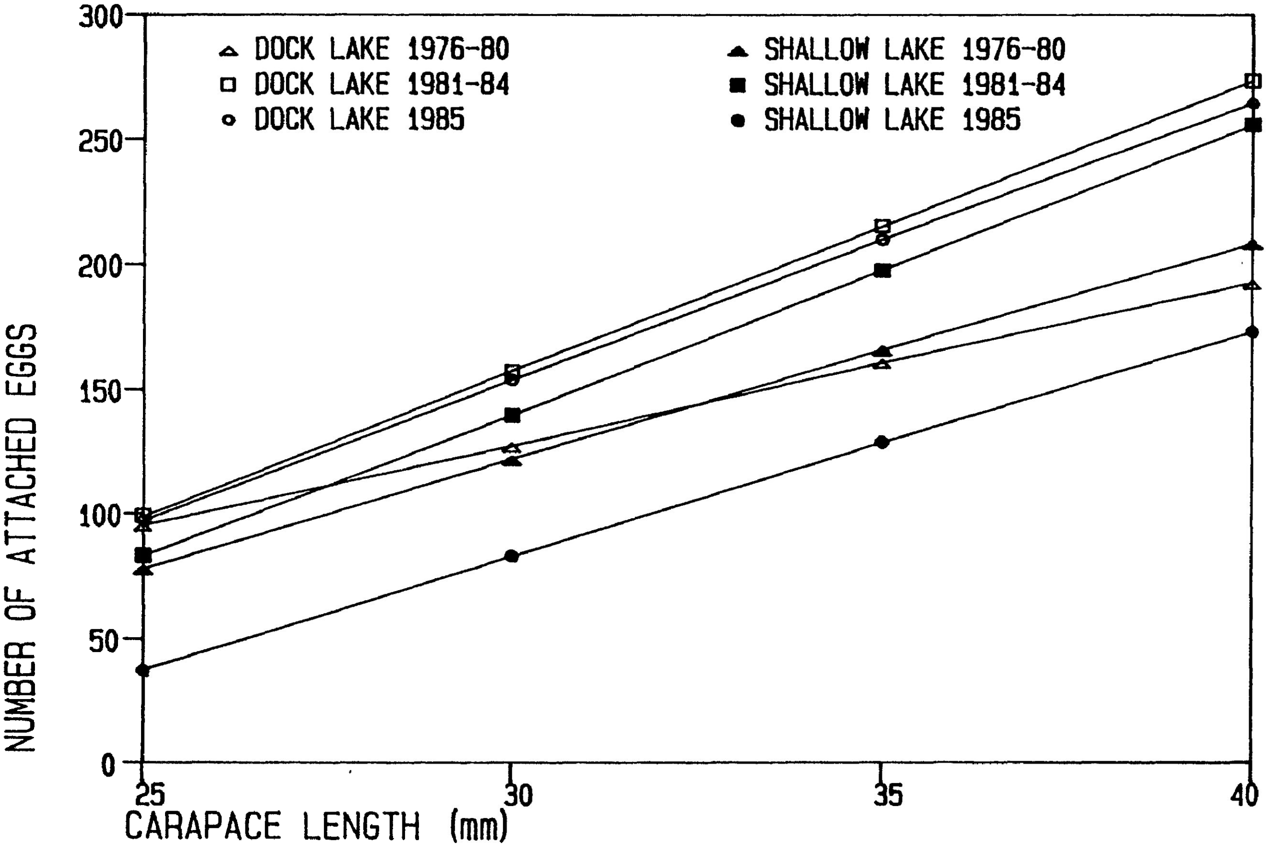
[1] Significance level for t-test of Ho: B = 0; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure 4. Relationships between carapace length (mm) and attached eggs of Dock and Shallow Lake females 1976-1980, 1981-1984 and 1985. Dock Lake linear regression lines, 1976-80: $Y=6.48X-66.68$, $R2=0.07$ $(P<001)$; 1981-84: $Y=11.68X-193.21$, $R2=0.19$ $(P<0.001)$; 1985: $Y=11.14X-180.83$, $R2=0.28$ $(P<0.001)$; Shallow Lake linear regression lines, 1976-80: $Y=8.71X-139.45$, $R2=0.10$ $(P<0.001)$; 1981-84: $Y=11.51X-205.16$, $R2=0.16$ $(P<0.001)$; 1985: $Y=9.10X-190.20$, $R2=0.12$ $(P<0.001)$, for relationship between number of pleopod eggs (Y) and carapace length (X).


△ DOCK LAKE 1976-80
□ DOCK LAKE 1981-84
○ DOCK LAKE 1985
▲ SHALLOW LAKE 1976-80
■ SHALLOW LAKE 1981-84
● SHALLOW LAKE 1985
NUMBER OF ATTACHED EGGS
0
50
100
150
200
250
300
25
30
35
40
CARAPACE LENGTH (mm)

84 ($P=0.54$). The 1985 yearlings in Shallow Lake however produced fewer eggs.mm^{-1} than in either Dock Lake ($P<0.001$) or Shallow Lake during 1976-84 ($P<0.001$).

Comparison of the 1985 females revealed that Shallow Lake yearling and mature females, regardless of age/size, produced about the same number of eggs.mm^{-1} ($P=0.19$) (Table 4). Dock Lake mature females however produced more eggs.mm^{-1} than did yearlings in 1985 ($P<0.003$).

Morphometric Relationships

We investigated the relationship between carapace length and number of attached pleopod eggs by using covariate analysis (Snedecor and Cochran 1967) pooling years into three intervals: 1976-80, 1981-84 and 1985. The relationship was linear over the sizes measured but carapace length only explained a small amount of variability in attached eggs (<1% to 46%; Table 5).

The 1976-80 length-attached eggs relationship was similar between Dock and Shallow Lake ($P>0.05$) (Table 5 and Fig. 4). The intercepts were significantly different between the lakes' relationships for 1981-84 ($P<0.025$) and also 1985 ($P<0.001$). The length-attached eggs relationship of 1976-80 Dock Lake females was significantly different from both 1981-84's slope ($P<0.01$) and intercept ($P<0.001$), and also 1985's slope ($P<0.05$) and intercept ($P<0.005$). The 1981-84 and 1985 Dock Lake relationships did not differ ($P>0.05$). Shallow Lake female length-attached eggs relationships differed only in intercepts between 1976-80 and 1981-84 ($P<0.025$), 1981-84 and 1985 ($P<0.01$) and 1976-80 and 1985 ($P<0.001$).

Table 6. Carapace length - weight relationships of females in Dock (harvest 1984, spring 1985 and harvest 1985) and Shallow Lake (spring 1985).

TABLE 6. Carapace length - weight relationships of females in Dock (harvest 1984, spring 1985 and harvest 1985) and Shallow Lake (spring 1985).

Year	Sampling Period	Lake	Independent Variable (X)	Dependent Variable (Y)	Slope[1] (b)	Intercept (a)	r	R^2	n
1984	Harvest	Dock	$\log_{10}$carapace length (mm)	$\log_{10}$wet weight (gm)	2.9950***	- 3.5681	0.99	0.97	91
1985	Spring Fecundity Sample	Dock	Carapace length (mm)	wet weight (gm)	0.6837***	-13.9125	0.97	0.94	117
		Shallow			0.7114***	-14.7908	0.96	0.93	118
		Dock	$\log_{10}$carapace length (mm)	$\log_{10}$total weight (gm)	3.0148***	- 3.6041	0.98	0.96	114
		Shallow			2.9670***	- 3.5456	0.97	0.93	69
		Dock	Carapace length (mm)	100.average egg weight (gm)	0.0134***	0.0693	0.37	0.14	114
		Shallow			-0.0026	0.6240	0.02	0.003	69
		Dock	Carapace length (mm)	relative fecundity	-0.6758***	45.3824	-0.28	0.08	114
		Shallow		(number of eggs) wet weight^{-1})	0.1864	10.3327	0.06	0.003	69
		Dock	Carapace length (mm)	weight of eggs (gm)	0.0725***	-1.4261	0.67	0.45	114
		Shallow			0.0583***	-1.2828	0.53	0.28	69

TABLE 6. (Cont'd)

Year	Sampling Period	Lake	Independent Variable (X)	Dependent Variable (Y)	Slope[1] (b)	Intercept (a)	r	R^2	n
1985	Spring Fecundity Sample (cont'd)	Dock	number of eggs. carapace length^{-1}	100.average egg weight (gm)	-0.0158**	0.5555	-0.23	0.05	114
		Shallow	(mm)		-0.0675**	0.7935	-0.36	0.13	69
	Harvest	Dock	$\log_{10}$carapace length (mm)	$\log_{10}$wet weight (gm)	2.9498***	-3.5014	0.99	0.99	103

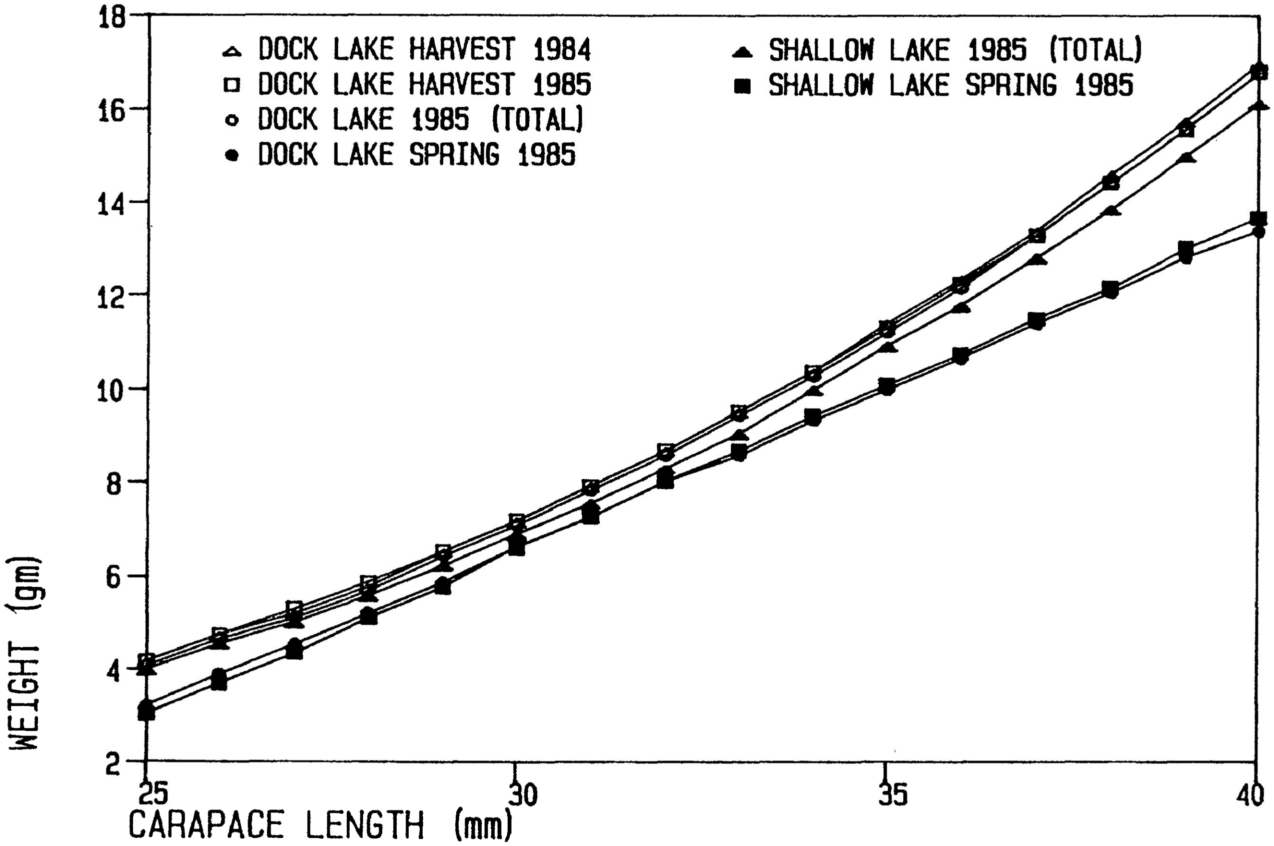
[1] Significance level for t-test of Ho: B = 0

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Figure 5. Relationships of carapace length and weight of Dock and Shallow Lake mature females 1985 and harvest 1984 and 1985 Dock Lake females. Dock Lake linear regression lines, 1984 harvest: $\log Y = 2.9950 \log X - 3.5681$, $R2 = 0.97$ ($P < 0.001$); 1985 spring: $\log Y = 3.0148 \log X - 3.6041$, $R2 = 0.96$ ($P < 0.001$); 1985 harvest: $\log Y = 2.9498 \log X - 3.5014$, $R2 = 0.99$ ($P < 0.001$), for relationship between logarithmically transformed (base 10) total wet weight (Y) and logarithmically transformed carapace length (X); 1985 spring: $Y = 0.6837X - 13.9125$, $R2 = 0.94$ ($P < 0.001$), for relationship between wet weight (i.e., total weight-weight of eggs) (Y) and carapace length (X). Shallow Lake linear regression lines, 1985 spring: $\log Y = 2.9670 \log X - 3.5456$, $R2 = 0.93$ ($P < 0.001$), for relationship between logarithmically transformed (Base 10) total weight (Y) and logarithmically transformed carapace length (X); 1985 spring: $Y = 0.7114X - 14.7908$, $R2 = 0.93$ ($P < 0.001$), for relationship between wet weight (i.e., total weight-weight of eggs) (Y) and carapace length (X).

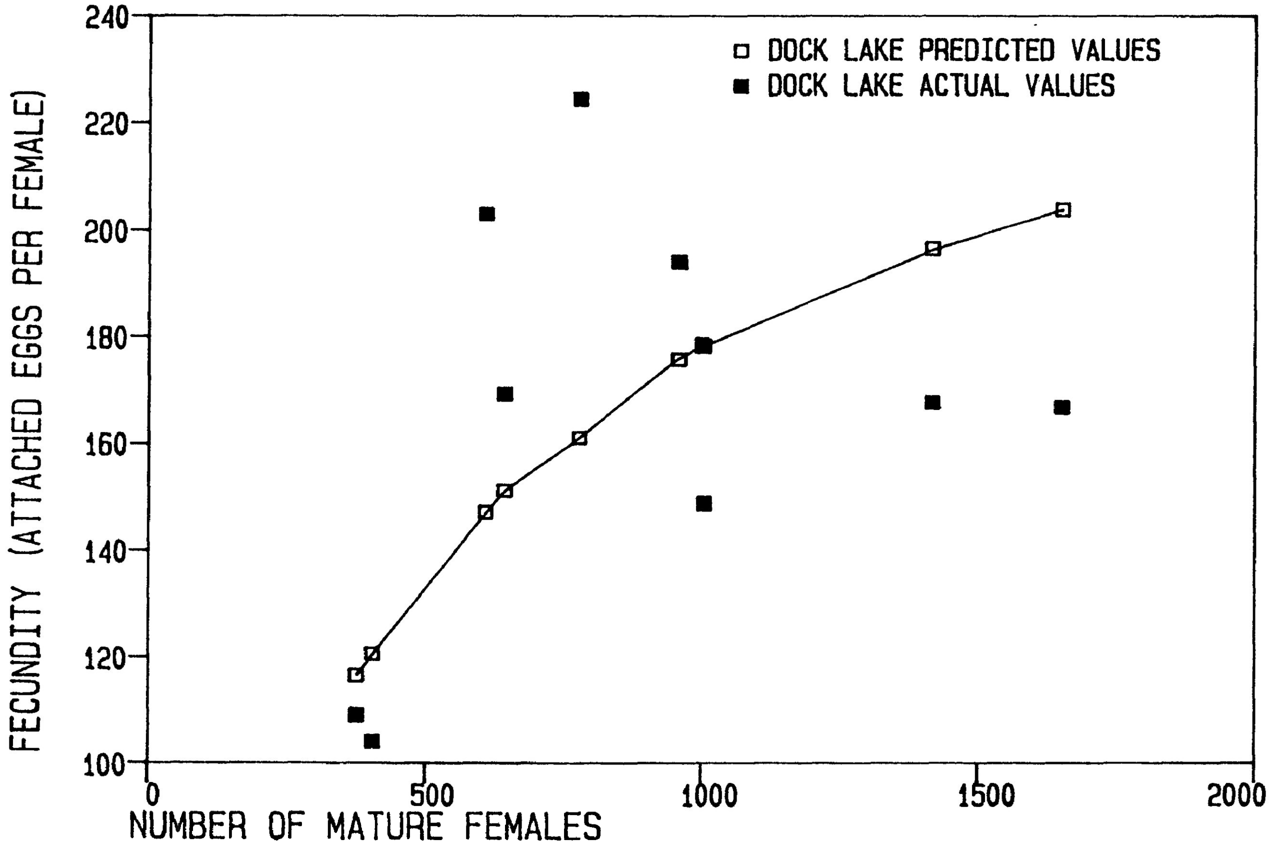

△ DOCK LAKE HARVEST 1984
□ DOCK LAKE HARVEST 1985
○ DOCK LAKE 1985 (TOTAL)
● DOCK LAKE SPRING 1985
▲ SHALLOW LAKE 1985 (TOTAL)
■ SHALLOW LAKE SPRING 1985
WEIGHT (gm)
CARAPACE LENGTH (mm)
2
4
6
8
10
12
14
16
18
25
30
35
40

Therefore per capita egg production of crayfish in Dock Lake increased between the 1976-80 period and the 1981-84 period (Fig. 4). Shallow Lake per capita egg production increased at the same time although less so than in Dock Lake females. In 1985 Dock Lake per capita egg production was similar to the 1981-84 period and significantly above that of Shallow Lake.

This between lakes disparity regarding the 1985 egg production was examined by analysing differences between: length, weight of eggs, number of eggs, and weight of females in both lakes (Table 6 and Fig. 5). Covariate analysis revealed no difference between the length-wet weight linear relationship of Dock and Shallow Lake fecund females ($P>0.05$). However the length-total weight (i.e., wet weight + weight of eggs) power relationship of fecund females showed a significant difference between intercepts ($P<0.005$). This resulted in a slightly positive linear relationship between carapace length and individual egg weight in Dock Lake females (Table 6). In addition relative fecundity (number of eggs.wet weight^{-1} of female) declined with increasing carapace length in Dock Lake (Table 6). As a result while a 24 mm female produced 29.16 eggs.gm^{-1} a 40 mm female would produce only 18.35 eggs.gm^{-1} in Dock Lake. Meanwhile Shallow Lake females produced, on average, only 16.10 eggs.gm^{-1} (standard deviation = 9.92, n=69). Consequently Dock Lake females produced more and heavier eggs.mm^{-1} at a lower energetic cost than did similar sized Shallow Lake females in 1985 (e.g., Table 6: number of eggs.mm^{-1}-average egg weight relationship).

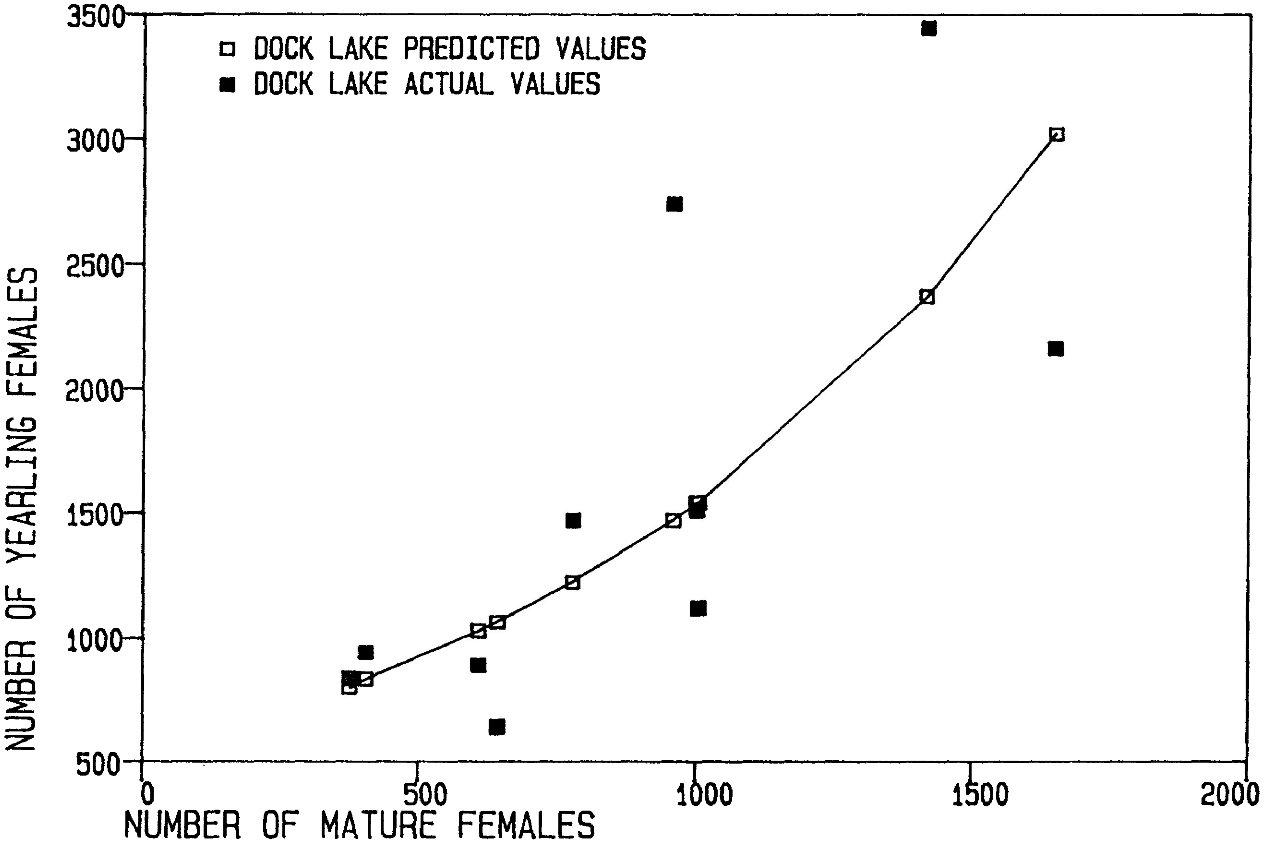
Apparently since there is no difference between the 1984 and 1985 harvest and the spring 1985 length-total weight power

Figure 6. Relationship between mature female density and fecundity in Dock Lake. Regression line, $1/Y=1.81226/X+0.00382$, $R2=0.54$ $(P<0.025)$, for relationship between fecundity (Y), measured as the number of attached pleopod eggs, and absolute density of mature, age I+ females (X) estimated during the spring period.



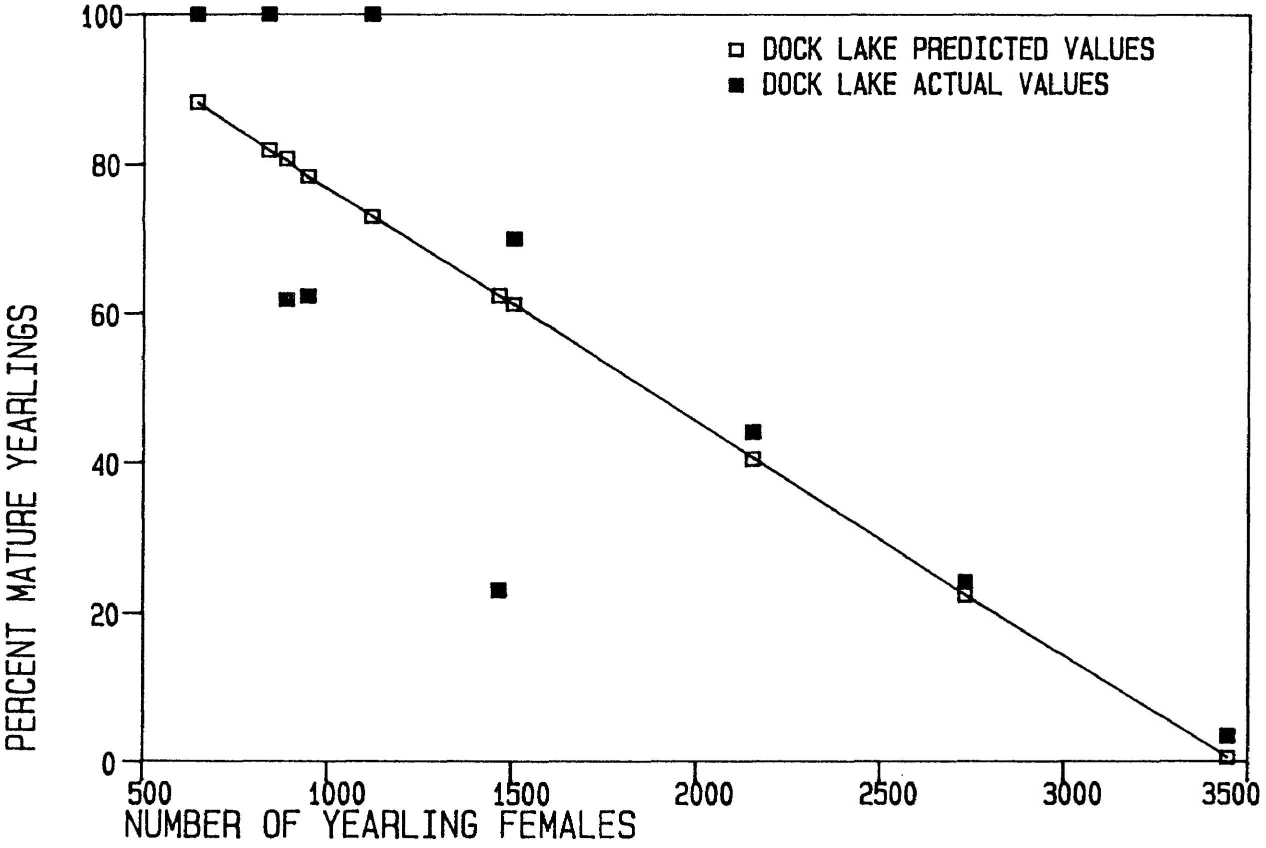
□ DOCK LAKE PREDICTED VALUES
■ DOCK LAKE ACTUAL VALUES
FECUNDITY (ATTACHED EGGS PER FEMALE)
240
220
200
180
160
140
120
100
0
500
1000
1500
2000
NUMBER OF MATURE FEMALES

Figure 7. Relationship between mature female density and yearling female density in Dock Lake. Regression line, $\ln Y=0.001036X+6.304$, $R2=0.61$ ($P<0.004$), for relationship between logarithmically transformed (Napierian logarithm) absolute density of yearling, age 0+ females (Y) and absolute density of mature, age I+ females (X) estimated during the spring period.



□ DOCK LAKE PREDICTED VALUES
■ DOCK LAKE ACTUAL VALUES
3500
3000
2500
2000
1500
1000
500
0
500
1000
1500
2000
NUMBER OF YEARLING FEMALES
NUMBER OF MATURE FEMALES

Figure 8. Relationship between yearling female density and percent of yearlings sexually mature in Dock Lake. Regression line, $Y=-0.03132X+108.2$, $R2=0.68$ ($P<002$), for relationship between the percent of sexually mature yearling, age 0+ females (Y) and absolute density of yearling, age 0+ females (X) estimated during the spring period.


DOCK LAKE PREDICTED VALUES
DOCK LAKE ACTUAL VALUES
PERCENT MATURE YEARLINGS
100
80
60
40
20
0
500
1000
1500
2000
2500
3000
3500
NUMBER OF YEARLING FEMALES

relationship of Dock Lake females (Fig. 5), summer growth principally manifests itself in the egg production of the following spring. Although exploited females in Dock Lake show a higher weight gain per unit of length than unfished Shallow Lake females, this results in the production of more and heavier eggs. Thus spent females in Dock and Shallow Lake of similar length weigh about the same. However after producing eggs, Dock Lake females gain back much of the weight lost during the reproductive cycle.

Fecundity Predictors

In Dock Lake the number of attached eggs.female^{-1} is a function of the number of mature females (Fig. 6). The number of yearling females is in turn related to the number of mature females (Fig. 7). However yearlings are comprised of both immature and mature individuals. The percent of sexually mature yearlings is negatively related to yearling density (Fig. 8). By estimating the number of mature females in the spring we can determine: (1) the fecundity of mature females, (2) the density of yearling females and (3) the number of mature yearling females (which translates into yearling fecundity by simply multiplying the number of mature yearlings by 108.1, the average number of $\text{eggs.yearling}^{-1}$).

Dock and Shallow Lake yearlings have the same average fecundity (Table 1 and 2) irregardless of density or yearly environmental variation. We therefore examined the role of possible abiotic factors influencing mature female fecundity with stepwise multiple regression analysis. The "step-down" procedure

Table 7. Stepwise multiple regression statisitcs of Dock Lake mature female fecundity 1976-1985 with abiotic factors (meteorological conditions for the month of May).

TABLE 7. Stepwise multiple regression statistics of Dock Lake mature female fecundity 1976-1985 with abiotic factors (meteorological conditions for the month of May).

Predictor Variables	Coefficients (b)	Student T Value	Significance	R^2
Number of Mature Females (X^{-1})	3.230	7.23	0.002	0.54
Growing-Degree-Days Above 10°C	0.0001416	7.76	0.002	0.61
Number of Days Above 10°C	-0.001216	-7.53	0.002	0.79
Number of Days of Rain	0.0002630	4.30	0.02	0.93
Mean Average Monthly Temperature (°C)	0.001031	2.89	0.04	0.98
Constant (a)	-0.001353	-0.66	0.54	

Degrees of Freedom = 4

Overall F = 34.61 ($p < 0.003$)

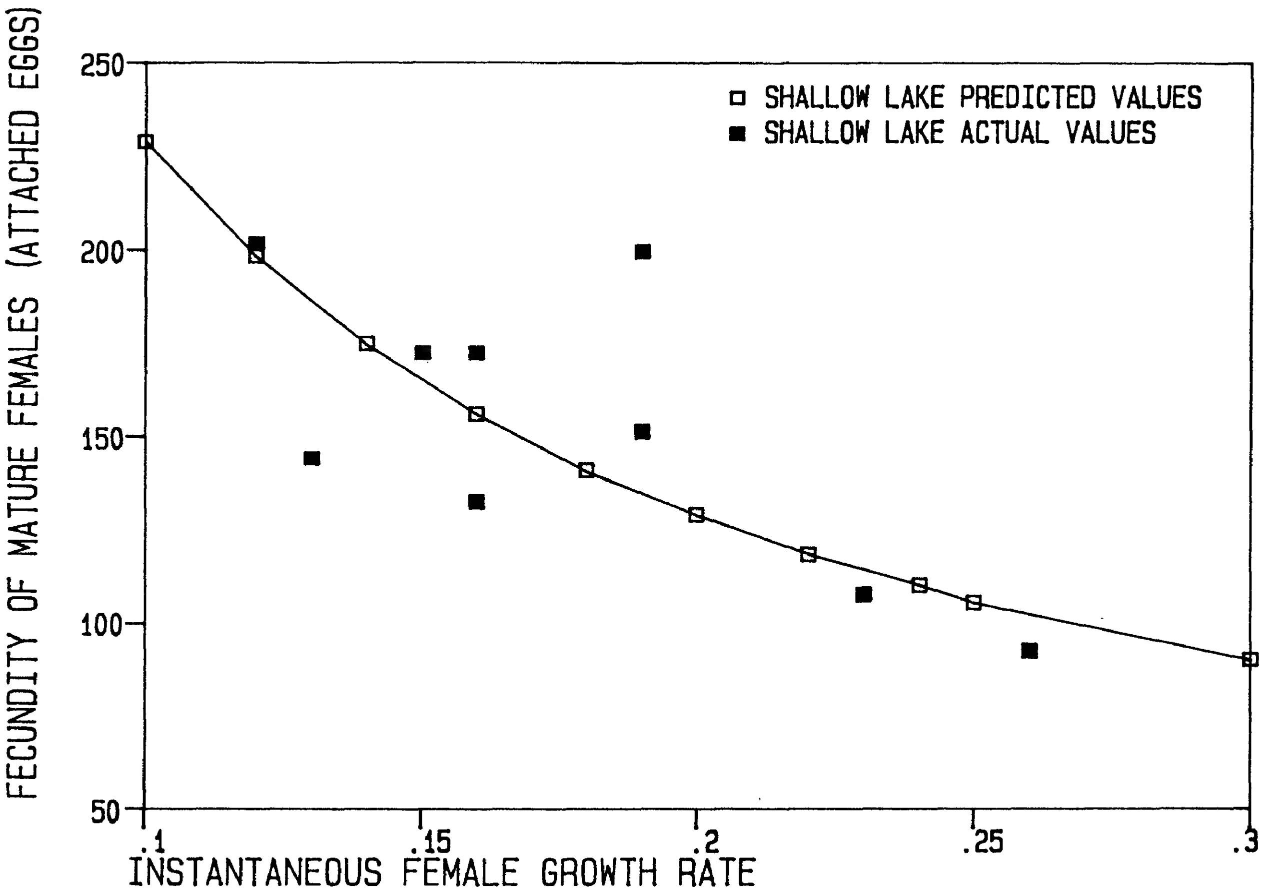
$r = 0.989$

$R^2 = 0.977$

Durbin-Watson Statistic for First-Order Autocorrelation = 1.57

Approximate Wilk-Shapiro Statistic = 0.77

Figure 9. Relationship between instantaneous growth rate of age I+-to-age II+ females (GI-II) and mature female fecundity in Shallow Lake. Regression line, $1/Y=0.03406X+0.0009604$, $R2=0.62$ ($P<0.007$), for relationship between mature female fecundity (time t+1) (Y) and growth rate during previous growing season (t) (X).

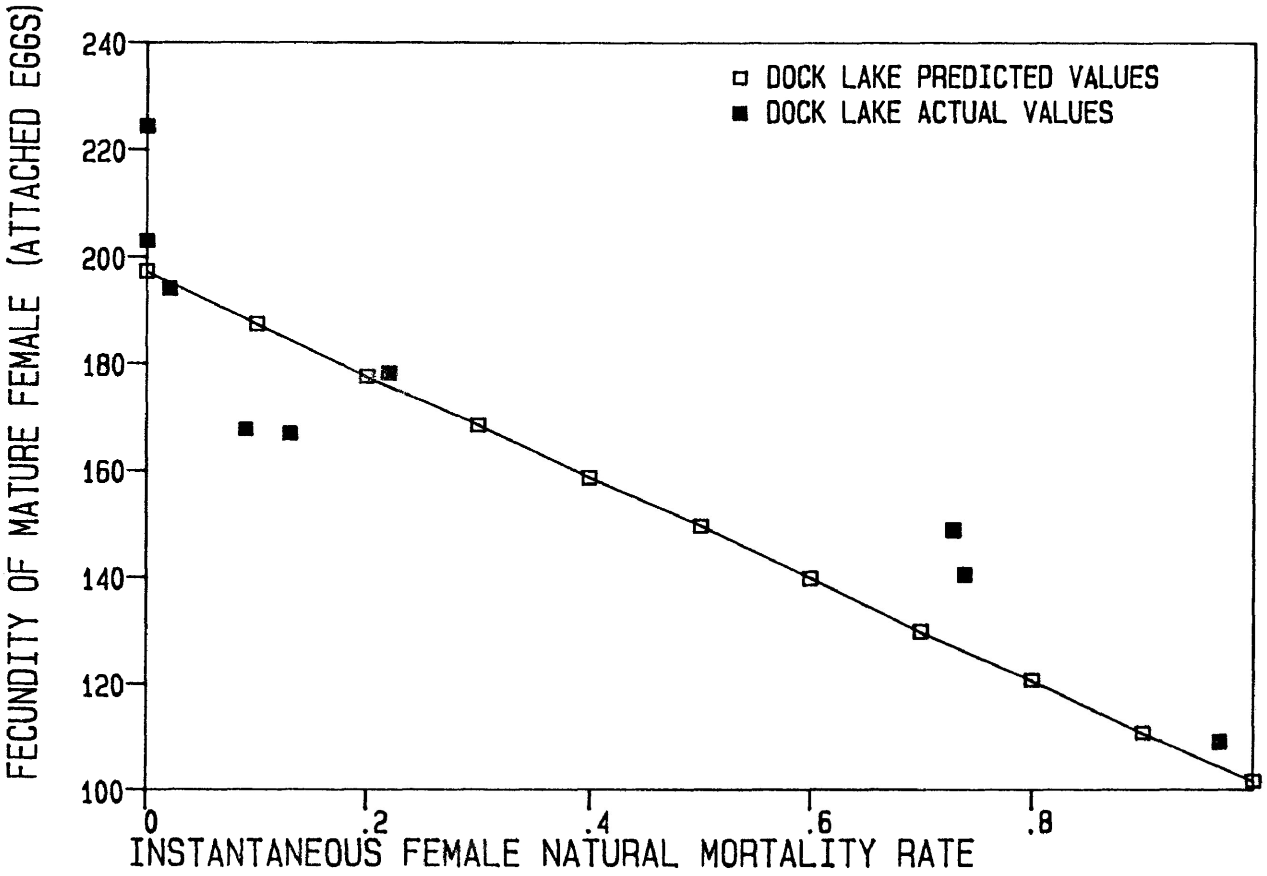


FECUNDITY OF MATURE FEMALES (ATTACHED EGGS)
250
200
150
100
50
□ SHALLOW LAKE PREDICTED VALUES
■ SHALLOW LAKE ACTUAL VALUES
.1
.15
.2
.25
.3
INSTANTANEOUS FEMALE GROWTH RATE

analysed the mature female fecundity relationship by eliminating non-significant independent variables from the equation (Zar 1974). The abiotic factors used measured heat input as follows: growing-degree-days above 10^{o}C; monthly average of daily growing-degree-days above 10^{o}C; coefficient of variation of growing-degree-days above 10^{o}C; number of days above 10^{o}C; and average monthly temperature, and precipitation: amount of rain and number days of measurable rain for the month of May when females extrude their eggs. In Dock Lake the mature female-fecundity equation explained 54% of the variablility (Fig. 6) by adding the abiotic factors we increased the amount of explained variation to 98% (Table 7). The Durbin-Watson test of first-order autocorrelation in the residuals proved inconclusive due to the "short" time-series (i.e., minimum sample size is 10). We therefore used the Wilk-Shapiro rankit plot (Shapiro and Francia 1972) which showed no autocorrelation to be present (Table 7). Also examination of residual plots indicated homogeneous variance for each of the predictor variables. The fecundity of either Shallow Lake mature or yearling females could not be predicted from either a density relationship or from abiotic factors.

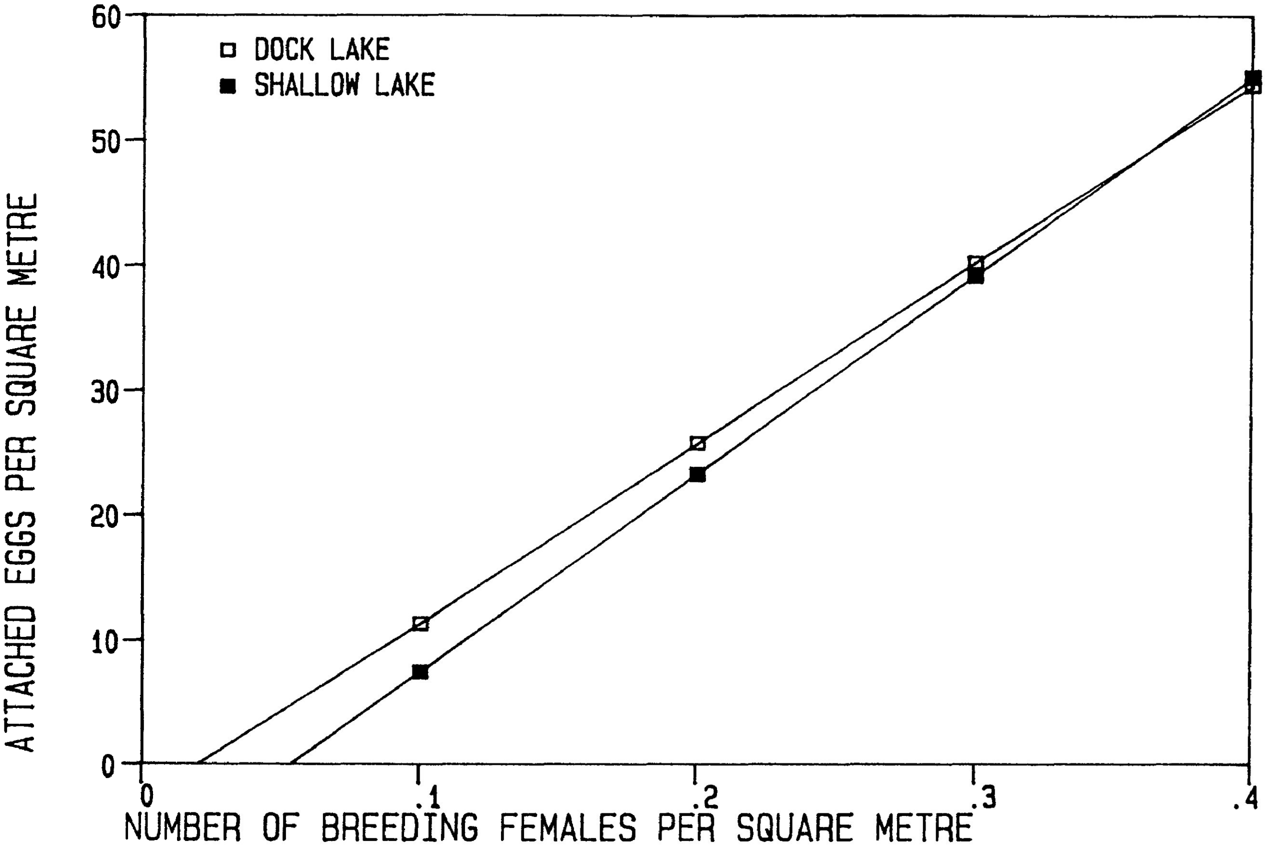
The possibility that mature female fecundity was related to growth or mortality, in either Dock or Shallow Lake, was also examined with a similar multiple regression analysis. Stepwise regression eliminated all abiotic parameters from the equation and showed that growth from age I-to age-II explained 62% of the variability in Shallow Lake mature female fecundity (Fig. 9). The stepwise regression of Dock Lake mature female fecundity also eliminated all abiotic factors but in contrast to Shallow Lake

Figure 10. Relationship between natural mortality rate of age I+-to-age II+ females (MI-II) and mature female fecundity in Dock Lake. Regression line, $Y=-95.63742X+196.94984$, $R2=0.81$ ($P<0.0005$), for relationship between mature female fecundity (time t+1) (Y) and natural mortality rate during previous growing season (t) (X).



□ DOCK LAKE PREDICTED VALUES
■ DOCK LAKE ACTUAL VALUES
FECUNDITY OF MATURE FEMALE (ATTACHED EGGS)
240
220
200
180
160
140
120
100
0
.2
.4
.6
.8
INSTANTANEOUS FEMALE NATURAL MORTALITY RATE

Figure 11. Relationship between the density of breeding females per m2 of littoral zone (<1.5 metres in depth) and the number of attached eggs per m2 in Dock and Shallow Lake. Dock Lake regression line, $Y=143.25339X-2.88423$, $R2=0.80$ ($P<0.0003$); Shallow Lake regression line, $Y=159.06225X-8.57084$, $R2=0.68$ ($P<0.002$), for relationship between egg production per m2 (Y) and density of breeding females per m2 (X).



□ DOCK LAKE
■ SHALLOW LAKE
ATTACHED EGGS PER SQUARE METRE
60
50
40
30
20
10
0
0
.1
.2
.3
.4
NUMBER OF BREEDING FEMALES PER SQUARE METRE

Figure 12. Relationship between the density of breeding females per m2 of littoral zone and the number of YOY per breeding female in Dock and Shallow Lake. Dock Lake regression line, $Y=-13.04876X+8.76946$, $R2=0.52$ ($P<0.03$); Shallow Lake regression line, $Y=-50.57275X+18.36355$, $R2=0.91$ ($P<0.0002$), for relationship between number of young-of-year per breeding female (Y) and density of breeding females per m2 (X).

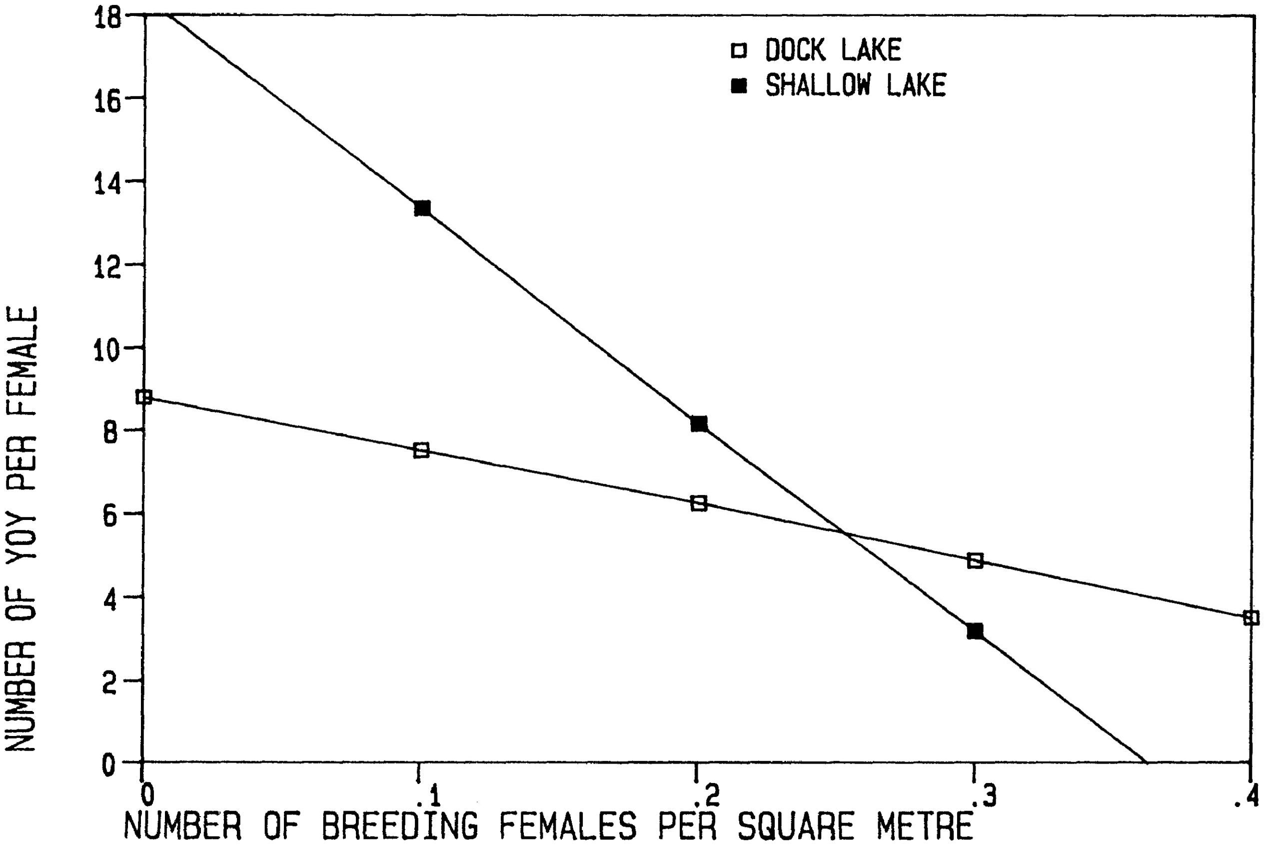

□ DOCK LAKE
■ SHALLOW LAKE
NUMBER OF YOY PER FEMALE
18
16
14
12
10
8
6
4
2
0
0
.1
.2
.3
.4
NUMBER OF BREEDING FEMALES PER SQUARE METRE

Figure 13. Relationship between the density of breeding females per m2 and the density of YOY per m2 in Dock and Shallow Lake. Shallow lake regression line, $Y=-4.18889X+1.99025$, $R2=0.65$ ($P<0.009$), for relationship between number of young-of-year per m2 (Y) and density of breeding females per m2 (X). Regression of similar relationship in Dock Lake was not significant, $Y=1.65447X+0.87116$, $R2=0.30$ ($P=0.08$), mean number of young-of-year per m2=1.30 (standard error=0.10).

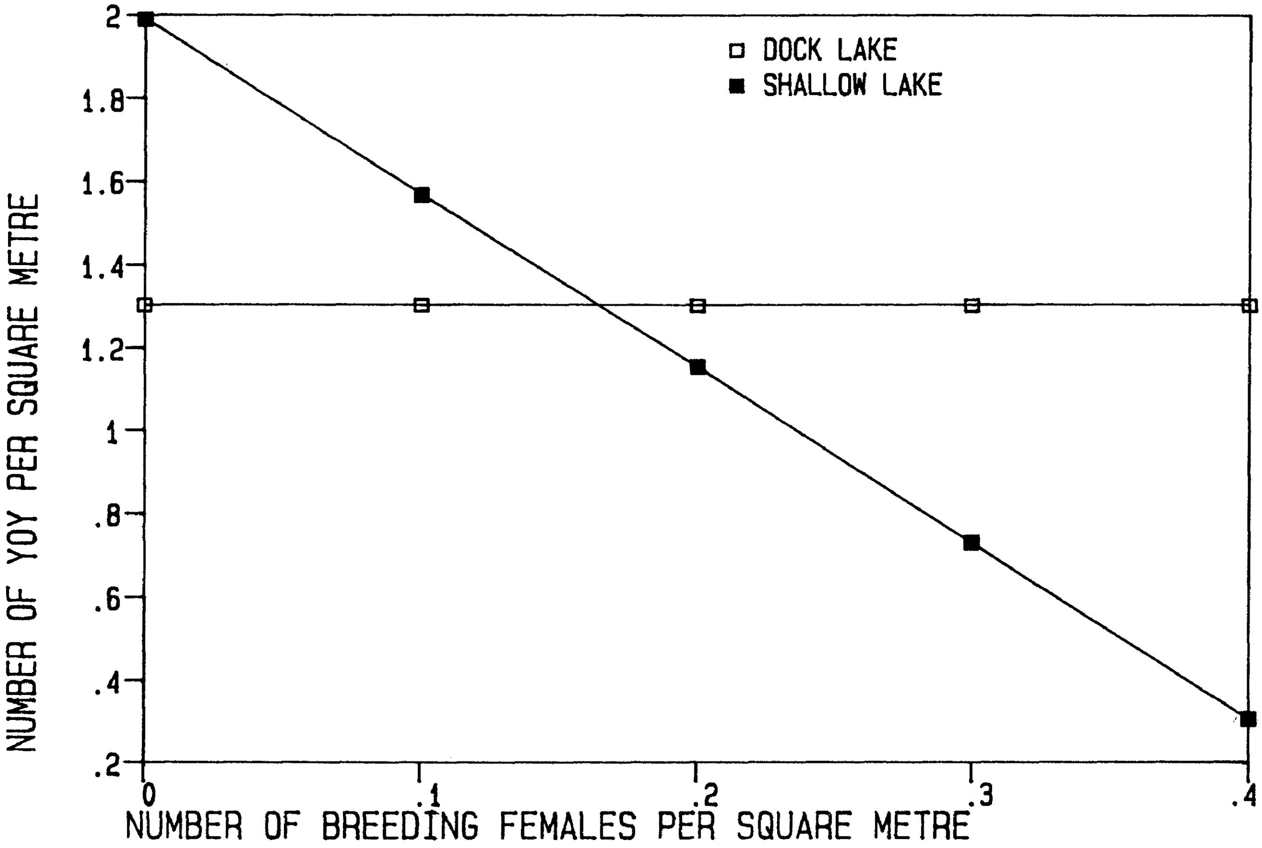

□ DOCK LAKE
■ SHALLOW LAKE
NUMBER OF YOY PER SQUARE METRE
2
1.8
1.6
1.4
1.2
1
.8
.6
.4
.2
0
.1
.2
.3
.4
NUMBER OF BREEDING FEMALES PER SQUARE METRE

Figure 14. Relationship between the percent survival from egg to YOY and initial density of attached eggs per m2 in Dock and Shallow Lake. Dock Lake regression line, $Y=-0.09454X+7.54285$, $R2=0.69$ ($P<0.006$); Shallow Lake regression line, $Y=-0.22806X+12.33369$, $R2=0.70$ ($P<0.005$), for relationship between percent survival from egg to young-of-year (Y) and egg production per m2 (X).

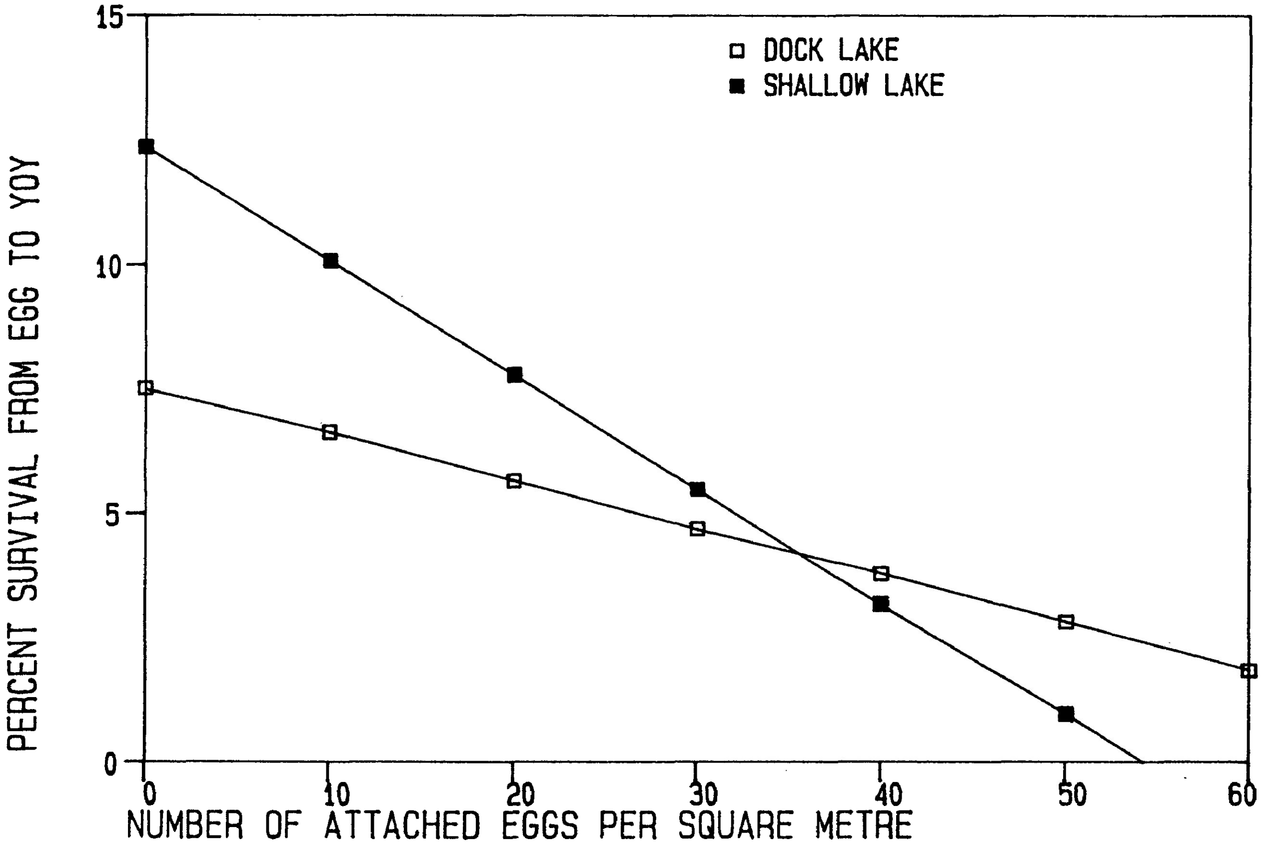

□ DOCK LAKE
■ SHALLOW LAKE
PERCENT SURVIVAL FROM EGG TO YOY
15
10
5
0
0
10
20
30
40
50
60
NUMBER OF ATTACHED EGGS PER SQUARE METRE

Table 8. Percent survival of Dock and Shallow Lake egg to YOY stage 1978-1985.

TABLE 8. Percent survival of Dock and Shallow Lake egg to YOY stage 1978 - 1985.

Year Interval	Lake	Survival from Egg to YOY (%)			
		Percent Male	Coefficient of Variation (%)	Female	Coefficient of Variation (%)
1978 - 1985	Dock	3.18	28.30	3.83	28.72
	Shallow	1.38	50.72	1.55	51.61

retained natural mortality from age I-to-age II as the predictor. This relationship explained 81% of the variability in fecundity (Fig. 10).

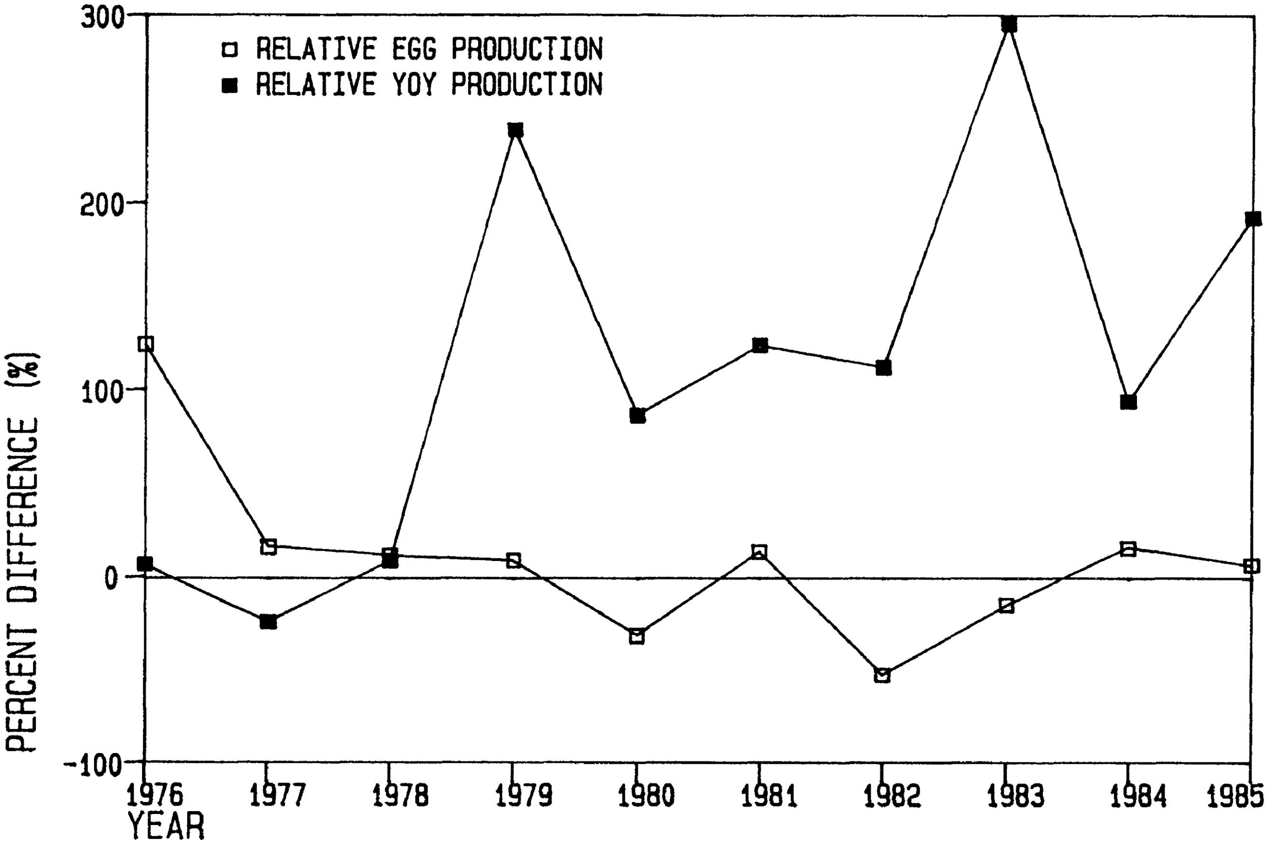
YOY Production and Recruitment Dynamics

Although exploitation increased mature female fecundity, it is the recruitment of free-living YOY that is far more important for maintenance of the population. Momot and Gowing (1977b) showed that density-dependent mechanisms strongly regulated the recruitment of YOY in unexploited Michigan populations even when large numbers of eggs were produced.

Dock and Shallow Lake reproductive potential proportionally increased with increases in female density (Fig. 11). This increase however failed to transfer into increased YOY production per female in either lake although the density-dependent mechanism appears more robust in Shallow Lake (Fig. 12). However by comparing the density of YOY with female density, we see that Dock Lake has a constant or slightly increasing production of $YOY.m^{2.-1}$ (available nursery habitat: Dock Lake = 6292 m^2; Shallow Lake = 8094 m^2) (Fig. 13). At comparably higher egg densities, survival from egg-to-YOY was higher in Dock Lake than in Shallow Lake (Figure 14). In Shallow Lake YOY survival is much more variable (Table 8).

After exploitation began, survival of YOY of both sexes significantly increased in Dock Lake (male: $P<0.004$; female: $P<0.003$). Furthermore no difference was seen in survival between sexes in either lake (Dock Lake: $P=0.29$; Shallow Lake: $P=0.69$). However the slight difference between egg-to-YOY survival in Dock

Figure 15. Time series of the percent difference between egg production per m2 and YOY per m2 in Dock and Shallow Lake 1976 to 1985. Relative differences are related to Shallow Lake parameters (i.e., positive values favour Dock Lake while negative values favour Shallow lake).



□ RELATIVE EGG PRODUCTION
■ RELATIVE YOY PRODUCTION
PERCENT DIFFERENCE (%)
300
200
100
0
-100
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

and Shallow Lake resulted in significant differences between relative egg production and relative YOY production (Fig. 15). Relative rates are measured with the difference expressed as a percentage of Shallow Lake's parameter. While Dock Lake egg production varied after 1977, being 15% greater to 53% less than in Shallow Lake, YOY production in this same period was from 9% to 296% greater! Therefore increased mature female fecundity, concomitant with adjustments in egg-to-YOY survival, resulted in constant YOY recruitment.$m^{2}.^{-1}$ in Dock Lake.

The production of YOY crayfish in Dock Lake apparently has maximized relative to available habitat (Fig. 13). For this particular northern crayfish stock, saturation density of YOY in littoral waters <1.5 m deep was approximately 1.30 YOY.$m^{2}.^{-1}$ (standard deviation = 0.280, n=8). Annually Dock Lake females produced between 7000-9500 YOY. At 4000 trap-days nominal effort, recruitment to the exploitable stock stabilized at approximately 5600 age I crayfish (1983-85 number of age I males: 2803, standard deviation = 528; number of age I females: 2779, standard deviation = 645). The maximum survival from YOY-to-age I (when year-class strength is determined in the exploited stock) is about 60-80% of the constant YOY production. The possibility of recruitment overfishing increases as exploitation removes proportionately more crayfish. In 1985 we increased the effort to 6000 trap-days and harvested 5558 crayfish from Dock Lake. This appears close to the maximal age I recruitment rate and we predict that borderline recruitment overfishing is now occurring in Dock Lake. At higher exploitation levels (e.g., 6000 trap-days effort) the catch becomes increasingly dependent on newly recruited age I crayfish. In such instances annual harvests become a good indicator of recruitment to that years exploitable stock. Therefore knowledge about the dynamics of the recruitment process is essential for effective crayfish stock management.

DISCUSSION

Over the past decade significant inter- and intra-population variation in reproductive characteristics has occurred. The increased levels of fishing effort since 1977 produced differences in total annual fecundity between lakes in 1981 and 1985. Since no decade long fecundity differences occurred in yearlings (age 0+), the changes must have instead centred in mature females (age I+). The age I+ females of 1976, 1981 and 1985 were produced from year-classes hatched during the coldest spring periods recorded during the entire study (less than 20 growing-degree-days >10°C) (Figure 3). Relative YOY production of the 1979 and 1983 year-classes also showed great discrepancies between Dock and Shallow Lake (Fig. 15). Thus cold springs not only affected YOY recruitment in Shallow Lake but also contributed to decreased mature female fecundity 2 years later. The environmentally forced time lags in Shallow Lake are manifested as: (1) an immediate effect on egg-to-YOY survival, (2) a reduction in future female fecundity potential, (3) a reduction in future egg quality and (4) a reduction in female weight growth potential. Although environmental factors do not strongly regulate annual egg production and recruitment, any significant deviation of spring weather from the climatic average does effect recruitment by producing a time delay response in the control lake's fecundity response. These previous cold springs may act through nutritional condition over the next 2 growing seasons and directly affect fecundity and/or egg quality.

Food availability relative to density may also effect fecundity. In a controlled experiment using females collected during the 1985 Dock Lake harvest, aquaria containing fertilized age 0+ and age I+ females were established at replications of low, medium and high densities (Lindsey 1986). These densities were based on empirical data collected from 1976 to 1985. The aquaria were maintained at temperature and photoperiod conditions necessary for maximal egg production (Aiken 1969). No significant fecundity differences were detected between yearlings or mature females held at various densities. However the fecundity of both groups fell significantly below that expected from empirical field data. Mature female fecundity decreased more than that of yearlings. There was also a significant difference between the 1985 length-wet weight of harvested females compared to the length-total weight of experimental animals. This compares with the difference observed in the spring of 1985 between Dock and Shallow Lake females. Since food and shelter was supplied ad libitum and density had no effect, the decrease must have been due to other factors; conceivably a pheromone induced physiological or behavioural feedback in the closed system of the aquaria (Mason 1970; Little 1976). The effect of a 12% to 16% loss of wet weight, for 25 mm to 41 mm CL sized females, respectively; significantly lowered fecundity. Physiological stress associated with growth may reduce realized fecundity to similar levels between first time and mature spawners.

Inhibited reproduction is also apparent within Shallow Lake mature females. Mature female fecundity is inversely related to age I-to-age II growth rate (Fig. 9). As a result reproductive effort in Shallow Lake is a function of available resources as expressed through the physiological condition of the female. This partitioning of energy towards reproduction is apparently balanced relative to somatic tissue requirements. This decreases egg output in favour of increased growth. A decrease in female moult increment following reproduction has been demonstrated in crayfish (Hopkins 1967; Brewis and Bowler 1982). In contrast the alteration of mean age-specific growth rates relative to future fecundity has never been documented. Apparently in Shallow Lake, female fecundity is regulated by summer food competition mediated through the growth response. Similar results have occurred in other species such as **Pacifastacus leniusculus** Dana and **Astacus astacus** Linne. Abrahamsson and Goldman (1970), and Abrahamsson (1972) demonstrated the influence of food supply on number and size of reproductive females in unexploited crayfish populations.

In unexploited Shallow Lake YOY recruitment was a linear function of the interaction between parental stock size, population fecundity and egg-to-YOY survival (Fig. 11 and 13, respectively). This resulted in strongly density-dependent YOY production. However the ambiguous pattern of reproductive traits was related to physiological constraints while the driving variable of recruitment rates was egg-to-YOY survival.

Since yearling female fecundity appears similar in both lakes, some physiological maximum must limit yearling egg production. If females grow to maturity in their first year then their fecundity becomes fixed within a narrow range (Tables 1, 2 and 4). The onset of female sexual maturity occurs at a mean carapace length of 24.3 mm (standard deviation = 1.00). Yearling females above this size produce on average 108 eggs. Considering the length of this study along with all of the possible complicating factors which could have effected yearling fecundity, the similarity between the two lakes and the consistency in temporal variation supports this hypothesis.

Exploited crayfish display direct density-dependent regulation of yearling numbers and indirectly, mature yearling female numbers. Spring heat energy budget of Dock Lake affects age I+ female fecundity (Table 7). In some studies the variability in fecundity resulted from spatial biological variation. In Trout Lake, Wisconsin, differences in temperature related to depth, influenced the percentage of female **Orconectes propinquus** (Girard) carrying eggs (Capelli and Magnuson 1974). But this decrease in the percentage of females bearing eggs was related to cooler temperatures found at increasing depths. No apparent difference was observed in the number of eggs.female^{-1}. In Lake Tahoe, low temperatures below 40 m affected the viability of **P. leniusculus** eggs (Abrahamsson and Goldman 1970). In our study temporal biological change can be influenced by deviations from 'normal' climatic patterns and does produce greater fecundity difference between unexploited and exploited populations. However significant variability over time in the annual age-/size-specific fecundity rate is more associated with natural mortality in exploited populations than with the extremes in annual temperature variation (Fig. 10).

Both natural and fishing mortality determines the number of mature females present in the spring in Dock Lake. In Dock Lake mature female fecundity is negatively related to natural mortality from age I-to-age II (Fig. 10). This mortality occurs after completion of the harvest. As a result exploitation of females reduces competition. Food supply is an unlikely limiting factor because: (1) Dock Lake is nutrient rich, (2) the harvest lasts until the end of the growing season, and at this time crayfish do not excessively feed because their bioenergetic requirements are lower (Jones and Momot 1981), and (3) the females gain back the weight expended on reproduction before autumn begins (Fig. 5). In Dock Lake the growth response displaces the period of regulation of mature female fecundity from summer to fall/winter. During this time competition for some unknown resource may occur.

Apparently between 1976-80 and 1981-84 mature female fecundity increased in both lakes. However this increase was greater in harvested Dock Lake. In addition to enhancement of fecundity the average size of the mature females also increased. During this same period the size of Shallow Lake females remained unchanged (Table 3). Thus a growth response in length of mature females occurred in Dock Lake.

The 1985 Dock Lake mature females were smaller than those of 1981-84 while in Shallow Lake females, no change was seen.

Comparing the 1985 length-total weight and length-attached egg relationships shows that females of a similar size were both heavier and produced more eggs in Dock Lake (Table 6 and Fig. 5). This increased weight in Dock Lake was converted into increased egg production as evidenced by the fact that the 1985 length-wet weight relationships did not differ between the lakes. Hence the variable fecundity of Shallow Lake females must relate to changes in growth (i.e., wet weight.mm^{-1}). This could be the result of the 2 year time lag from the cold spring of 1983 (8.7 growing-degree-days >10 ^{o}C). Dock Lake females produced heavier eggs per unit of length at much less of an energetic cost than Shallow Lake females in 1985 (Table 6). Exploiting Dock Lake females apparently supplants the effect of environmental influences on growth, buffering both fecundity and juvenile recruitment against temperature fluctuations. Therefore we believe that temperature acts as a controlling factor, while food limits per capita reproductive responses.

Increased relative YOY production results from the positive relationship between carapace length and average egg size in 1985 Dock lake females (Fig. 15). This relationship was a response to exploitation which has conceivably contributed to increased YOY survival since 1978. However the direct relationship between egg size and survival is unknown. Large egg size may confer an advantage to survival. Mason (1978) found the same relationship between increasing female size and increasing egg size in P. leniusculus. More importantly the larger eggs produced significantly larger stage 2 young. Although survival and growth of stage 2 young varied considerably he showed a weak size related relationship (Mason 1978). Our study demonstrates the importance of such slight differences in survival (Table 8).

The relative increase in Dock Lake YOY production was the result of constant recruitment.m$^{2.-1}$, rather than increased egg production (Fig. 11, 13 and 15). Increased recruitment saturated available habitat obscuring both the underlying relationships and intraspecific factors influencing YOY production. The maintenance of high YOY production with increased female density resulted from adjustments in egg-to-YOY survival rates. This in turn was a consequence of increased egg size as a result of the changed growth function caused by exploitation. Dock Lake female crayfish thus circumvented food shortages which normally regulate a natural population's ability to produce eggs and young. This YOY recruitment response occurred as exploitation of age I+ female crayfish exceeded 25%, however the fecundity response wasn't detected until age I+ female exploitation exceeded 30%. Concurrently, total female exploitation rates of 30% increased YOY production and fecundity responses only occurred when exploitation rates exceeded 40%. For management of crayfish stocks, and possibly other crustaceans, we can safely harvest 30-40% of the female population without detrimentally effecting fecundity or future recruitment.

The fecundity response of Dock Lake mature females occurred 4 years after YOY recruitment increased (Fig. 15). Apparently adult exploitation initially affected YOY production. YOY recruitment was likely influenced by intrinsic or extrinsic factors operating independent of female fecundity. Mature female fecundity responded only after 40% of the females were removed by the fishery.

Exploited crayfish evidently do not significantly respond by altering their population reproductive effort but rather exhibit age-specific reproductive plasticity. Although per capita mature female fecundity significantly varies between lakes, annual total egg production, relative to available nursery habitat, is similar (Fig. 15). Since annual age-specific population densities differ and no exploitation response has been detected, extrinsic factors must independently control total egg production. This annually limits population fecundity to comparable levels in both lakes. Surprisingly, despite the high biological potential of crayfish, the expected increase in gross annual reproductive rate operating concurrently with the density-dependent per capita fecundity response, has not occurred. Apparently restructuring of age-specific fecundity contributions annually limits population fecundity relative to female density (Fig. 11). From our analysis we conclude that fecundity is not a regulatory mechanism in crayfish population dynamics. Although variations in population fecundity are linked to changes in female density, increased fecundity is not related to increased YOY production. This study supports Momot and Gowing's (1977a) contention that increased YOY production is the result of higher egg-to-YOY survival rates.

Several relationships may serve as possible indicators of crayfish demographic vigour (Table 6). These include between lake differences in: carapace length-average egg size, carapace length-relative fecundity, and number of eggs.mm^{-1}-average egg size. Management of exploited stocks could be facilitated simply by sampling fecund females, thus allowing for the detection of YOY production failures. We suggest that fecundity responses to perturbation are manifested in two ways: first by changing numbers (per capita fecundity) and secondly by the quality of pleopod eggs produced (relative fecundity). For example, Mason (1978) noticed that the Pitt Lake and Cowichan River stocks of P. leniusculus showed a positive relationship between egg size and size of female. However "the diameter of egg was decidely independent of maternal carapace length" in Shawnigan Lake (Mason 1978). The three populations showed similar carapace length-attached egg relationships. The main difference being that Shawnigan lake was a "eutrophying environment" and the population was "rather dense" (Mason 1978) suggestive of the conditions in Shallow Lake. An alternate method of determining population status would be to use the eggs.mm^{-1} ratio as an index of fertility. Stressed populations appear to have decreased age-specific egg production and display slight, if any, difference between yearling (first-time spawners) and mature female eggs.mm^{-1} ratio.

The fecundity response resulted in maximal YOY production limited by available habitat. However at high levels of exploitation, the nursery bottleneck in the population dynamics of Dock Lake crayfish predisposes the stock to recruitment overfishing. Therefore as crayfish populations are severely harvested, monitoring recruitment becomes necessary. An alternate management strategy would be habitat enhancement of the nursery area. Currently we are investigating the importance of nursery habitat (i.e., substrate and aquatic macrophytes) related to YOY density interactions and hope to increase YOY production using substrate modification techniques.

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GROWTH

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ABSTRACT

The principal response of Dock Lake's crayfish population to increased exploitation has been an increase in the mean female instantaneous growth rate during the young-of-year (YOY)-to-age I life stage. By removing one-third or more of the exploitable stock we produced a growth response. Size selective exploitation apparently removed the faster growing males, in terms of length and weight when compared to expected growth rates based on the 1976 baseline length-wet weight relationship. Growth during the egg-to-YOY life stage is density-dependent on adult population size. Most likely it is related to the quality/quantity of a seasonal food source. Cohort age- and sex-specific growth rates are regulated by initial YOY size. This growth pattern results in a dual size equilibria (i.e., same size age I, age II and age III adult crayfish from different size YOY). This is unrelated to stochastic variation in climatic parameters. Detection of growth overfishing is impossible. This is because the limited growth response is related to the determinate growth pattern produced by the labile YOY size/cohort growth rate interaction. Management guidelines to optimize growth and population density are discussed.

INTRODUCTION

An interaction between moult increment and moult interval results in the discontinuous growth pattern of crustaceans; separation of these factors is complicated by both temporal variation and individual variation (Brewis and Bowler 1982). The study of both intrinsic and extrinsic influences on individual moult increment and moult interval is necessary for a proper understanding of the growth process. However the operational outcome of these mechanisms is a difference in size from year to year, which becomes important in assessing changes in age- or sex-specific growth. Insight into population dynamics as well as yield assessment for management of exploited stocks requires an understanding of variation in mean "population" growth patterns.

The growth of the crayfish **Orconectes virilis** (Hagen) can be related to system productivity (Momot and Jones 1976; France 1985) and nutrient availability (Momot 1984). Many studies of crayfish are by necessity short-term (less than one generation in length) and so provide limited information on temporal growth incongruities. The choice of growth patterns based on assumed stable or stationary population characteristics is not sufficient. Among other things, one must consider the resilience of growth responses to variations in both environmental and population parameters.

As part of a long-term crayfish study in northwestern Ontario we examined the temporal variation in mean sex- and age-specific growth patterns. An opportunity to measure the long-term growth response of a crayfish population to severe levels of fishing intensity over a ten year period was provided by our experimental fishery.

STUDY AREA AND METHODS

We intensively studied populations of **Orconectes virilis** in two marl lakes in northwestern Ontario. Crayfish in Dock Lake have been harvested since 1977, the intention being to over-exploit the stock while comparing it's growth response to that of an unexploited population in nearby Shallow Lake. The physical and chemical properties of these marl lakes and the general methods employed have been described elsewhere (Momot 1978; Morgan 1987); only additional methods pertinent to this aspect of the study are described herein.

We employed size frequency polygons and modal progressions of previously marked animals of known age captured during a mark-recapture study and subsequent harvest period to delineate age-classes within the populations. All captured yearling, adult and approximately 100 to 400 young-of-year (YOY) were measured to the nearest 0.5 mm from the tip of the rostrum to the posteriomedial edge of the carapace using vernier calipers. All third stage instar YOY (age 0) were assumed to be 3.5 mm in length. This is the size at which they become independent of the female (Weagle 1970). Length or size refers to carapace length (CL) in mm. Mean age- and sex-specific growth rates were determined by following size modes that correspond to age-classes through plots of size distribution for sequential years until the end of a cohorts life span (3.5 years). The instantaneous growth rate (G) was calculated from sequential mean size estimates. The time interval between estimates for crayfish age 0+ (YOY) and older was 1 year, thus the calculated G value represents an annual mean instantaneous growth coefficient. The lack of annual length-weight data meant that length was used instead of weight for the calculation of G. However the estimation of weight growth can be derived using b, the slope, of the length-weight power relationship (Ricker 1975, pg. 207).

Seasonal length-wet weight relationships of the population in Dock Lake were computed from data collected in 1976, and during the harvests of 1984 and 1985. The 1984 carapace length-wet weight relationship was determined from 91 females (23 to 43 mm CL) and 96 males (23 to 51 mm CL). In 1985, 103 female crayfish (21 to 43 mm CL) and 122 males (22 to 47 mm CL) were measured and weighed. All crayfish were randomly selected from the trap catches during the harvest. Only individuals with intact appendages were sampled. The carapace length (mm) to wet weight (gm) relationships conformed to the power curve which were logarithmically transformed to allow linear regression. Analysis of covariance (Snedcor and Cochran 1967) determined any differences between-sex comparisons and between-year comparisons, particularly with the pre-harvest 1976 baseline length-wet weight relationship (Momot unpublished data; 146 males (25 to 45 mm CL) and 31 females (25 to 35 mm CL), using pooled means for each mm size class). Wilcoxon matched-pairs signed-ranks test (Daniel 1978) compared mean growth rate differences between lakes and sexes.

Table 1. Relationship between carapace length (mm) and wet weight (gm) for male and female crayfish in Dock Lake 1976 (Momot unpublished data), 1984 and 1985 harvests.

TABLE 1. Relationship between carapace length (mm) and wet weight (gm) for male and female crayfish in Dock Lake, 1976 (Momot unpublished data), 1984 and 1985 harvests.

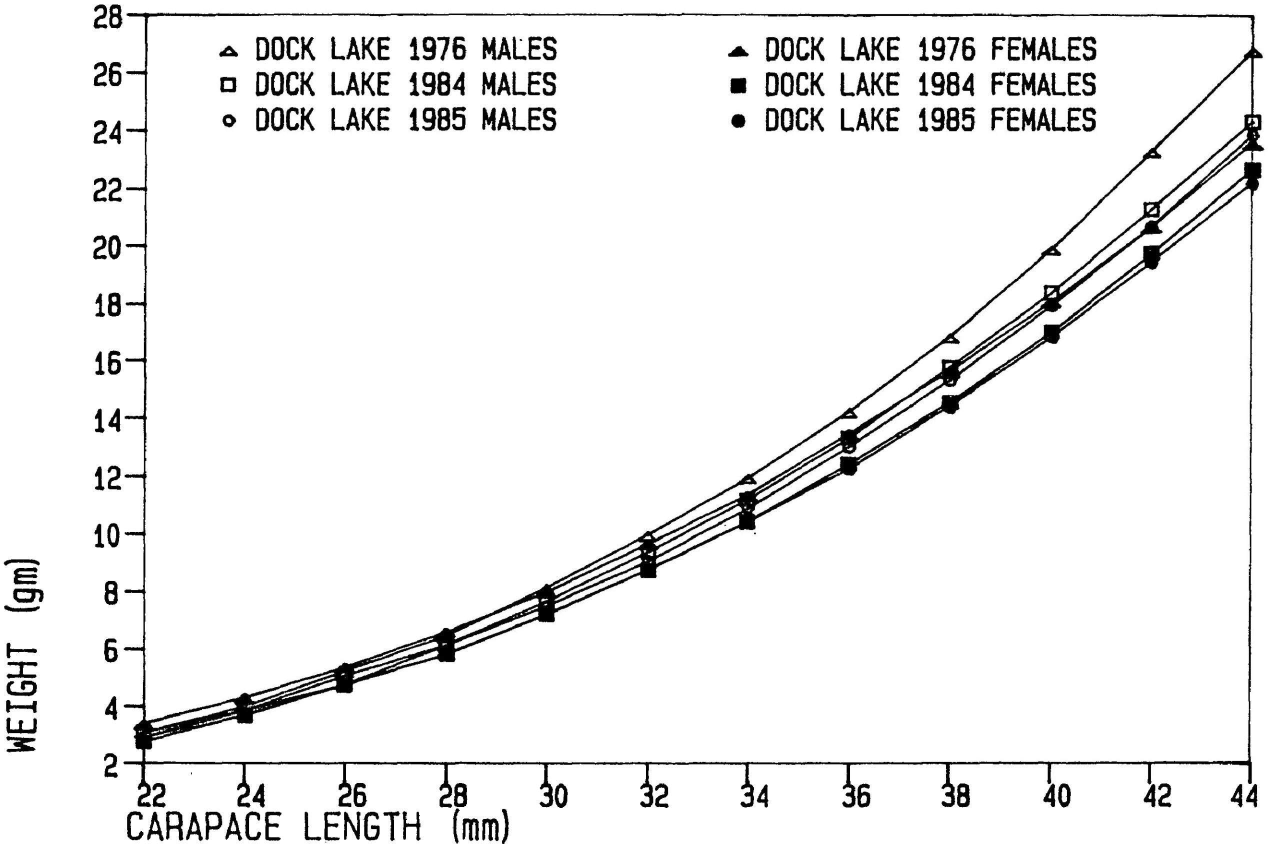
Year	Sex	Slope (b)[1]	Geometric Mean Slope[2]	Intercept (a)	Geometric Mean Intercept[3]	R^2	Sample Size (n)	Mean $log\ l$	Mean $log\ w$
1976	M	3.130710	3.142841	-3.717305	-3.736004	0.99	21	1.5374	1.0958
	F	2.799851	2.871878	-3.231018	-3.337258	0.95	11	1.4747	0.8979
1984	M	3.016007	3.051064	-3.569893	-3.623588	0.98	96	1.5351	1.0601
	F	2.995047	3.038436	-3.568087	-3.633877	0.97	91	1.5136	0.9651
1985	M	3.031227	3.047991	-3.603801	-3.629310	0.99	122	1.5255	1.0204
	F	2.949760	2.965745	-3.501430	-3.525406	0.99	103	1.4945	0.9069

[1] All regressions significant at p 0.00001 (Ho: B = 0) for $log\ w = a + b\ (log\ l)$ or $w = 10^{a} l^{b}$

[2] $b_{GM} = b/r$

[3] $a_{GM} = log\ \bar{w} - b/r\ (log\ \bar{l})$

Figure 1. Relationship between carapace length (mm) and wet weight (gm) for Dock Lake male and female crayfish 1976 (Momot unpublished data), 1984 and 1985 harvests. Linear regression lines, male 1976: logY=3.130710logX-3.717305, R2=0.99 (P<0.00001); female 1976: logY= 2.799851logX-3.231018, R2=0.95, (P<0.00001); male 1984: logY=3.016007logX-3.569893, R2=0.98 (P<0.00001); female 1984: logY=2.995047logX-3.568087, R2=0.97 (P<0.00001); male 1985: logY=3.031227logX-3.603801, R2=0.99 (P<0.00001); female 1985: logY=2.949760logX-3.501430, R2=0.99 (P<0.00001), for relationship between logarithmically transformed (base 10) weight (Y) and logarithmically transformed carapace length (X).



△ DOCK LAKE 1976 MALES
□ DOCK LAKE 1984 MALES
○ DOCK LAKE 1985 MALES
▲ DOCK LAKE 1976 FEMALES
■ DOCK LAKE 1984 FEMALES
● DOCK LAKE 1985 FEMALES
WEIGHT (gm)
2
4
6
8
10
12
14
16
18
20
22
24
26
28
CARAPACE LENGTH (mm)
22
24
26
28
30
32
34
36
38
40
42
44

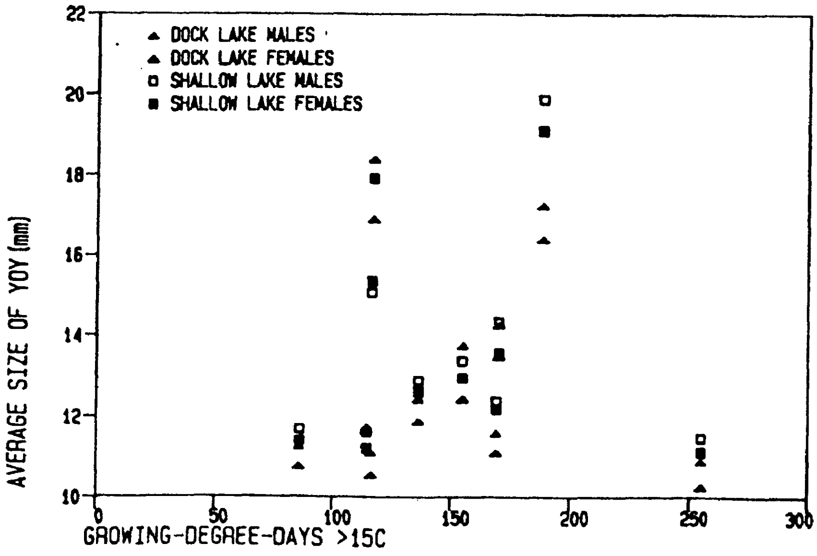
RESULTS

Length-wet Weight Relationships

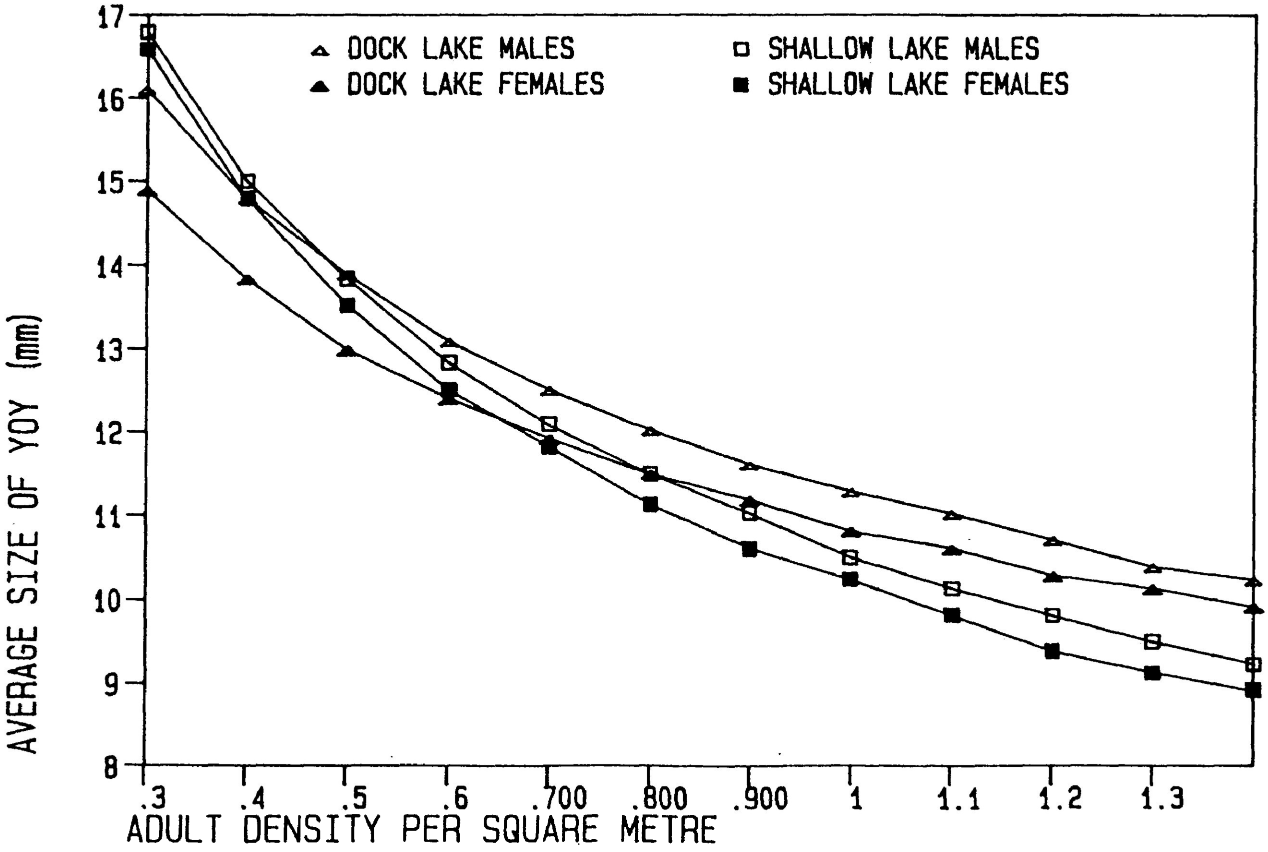
Wet weights (gm) were linearly related to carapace lengths (mm) of Dock Lake male and female crayfish using the log/log power transformation (Table 1). Males were significantly heavier than females in 1976, 1984 and 1985 (Fig. 1). The regression equations differed for slope between sexes in 1976, 1984 and 1985 ($P<0.001$); intercepts also differed between males and females in 1984 and 1985 ($P<0.001$).

Male growth significantly decreased between 1976 and 1984-85. The male regression equations differed significantly for slope ($P<0.025$) and intercept ($P<0.01$) between 1976 and 1984-85; there was no difference between 1984 and 1985 regression equations. While the disparity in male growth increased at the onset of sexual maturity (32.8 mm, standard deviation = 2.66) between 1976 and 1984-85, female growth remained unchanged (Fig. 1). The small 1976 female sample is insufficient to detect changes in the length-wet weight relationships between years (i.e., statistically inconclusive). However the slopes of the female regression equations were significantly different between 1984 and 1985 ($P<0.01$). Males thus have higher allometric growth rates than females (b of the length-weight relationship greater or less than 3; Ricker 1975, pg. 209). Overall, male length-wet weight growth rates have declined between 1976 and 1984-85 in Dock Lake (Table 1 and Fig. 1).

Figure 2. Relationship between young-of-year (YOY) size (mm) and adult density per m2 of littoral zone <1.5 m depth in Dock and Shallow Lake 1976 to 1985. Also YOY size and growing-degree-days >15oC during the same time period (inset). Dock Lake linear regression lines, male: lnY=-0.29761lnX+2.42240, R2=0.62 (P<0.004); female: lnY=-0.26655lnX+2.38347, R2=0.56 (P<0.007); Shallow Lake linear regression lines, male: lnY=-0.38914lnX+2.35419, R2=0.65 (P<0.003); female: lnY=-0.40646lnX+2.31976, R2=0.67 (P<0.002), for relationship between logarithmically transformed (Napierian logarithm) size of young-of year (Y) and logarithmically transformed adult population density per m2 (X).

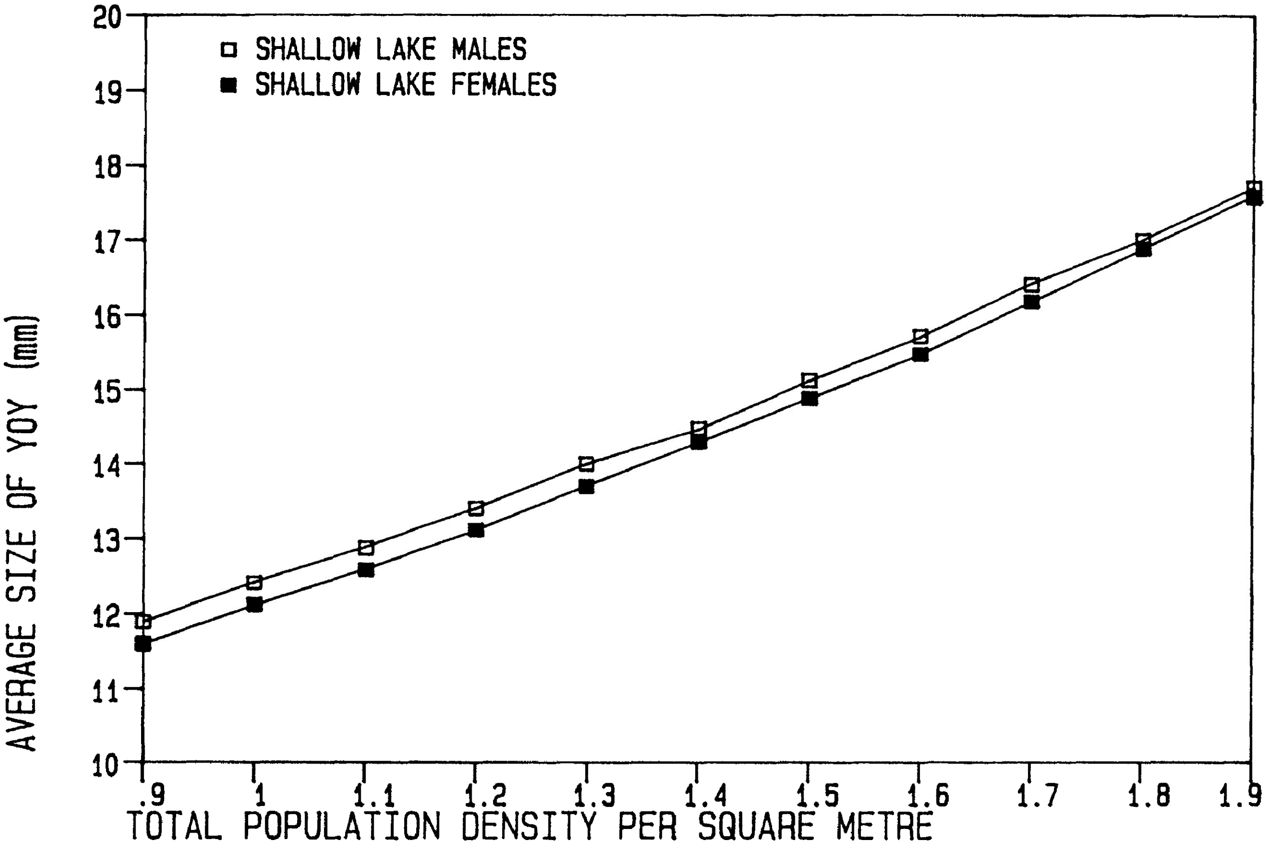


DOCK LAKE MALES
DOCK LAKE FEMALES
SHALLOW LAKE MALES
SHALLOW LAKE FEMALES
AVERAGE SIZE OF YOY (mm)
GROWING-DEGREE-DAYS >15C
22
20
18
16
14
12
10
0
50
100
150
200
250
300



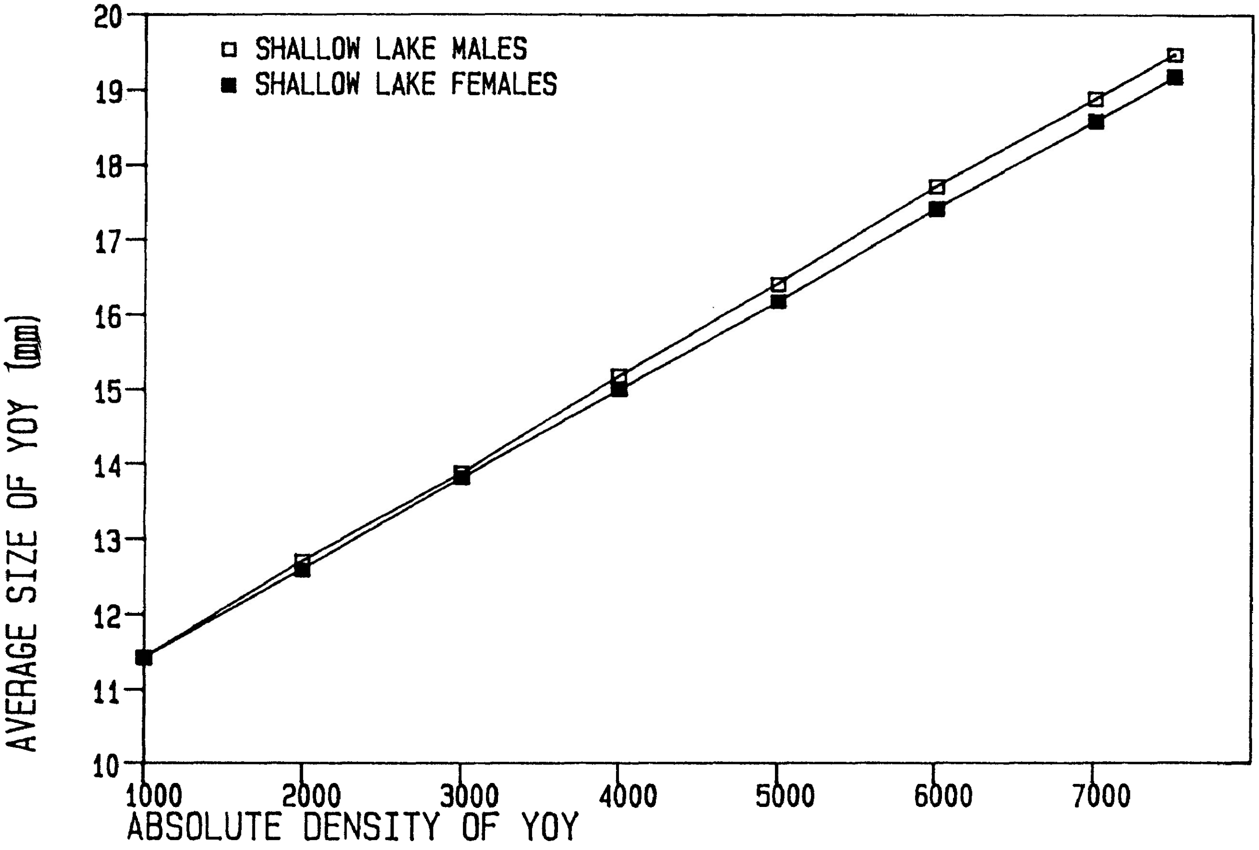
DOCK LAKE MALES
DOCK LAKE FEMALES
SHALLOW LAKE MALES
SHALLOW LAKE FEMALES
AVERAGE SIZE OF YOY (mm)
ADULT DENSITY PER SQUARE METRE
17
16
15
14
13
12
11
10
9
8
.3
.4
.5
.6
.700
.800
.900
1
1.1
1.2
1.3

Figure 3. Relationship between YOY size and total density per m2 (i.e., adult density + YOY density) in Shallow Lake 1976 to 1985. Linear regression lines, male: $\ln Y=0.39496X+2.12459$, $R2=0.61$ ($P<0.004$); female: $\ln Y=0.41889X+2.07187$, $R2=0.66$ ($P<0.003$), for relationship between logarithmically transformed (Napierian logarithm) size of young-of-year (Y) and total population density per m2 (X).



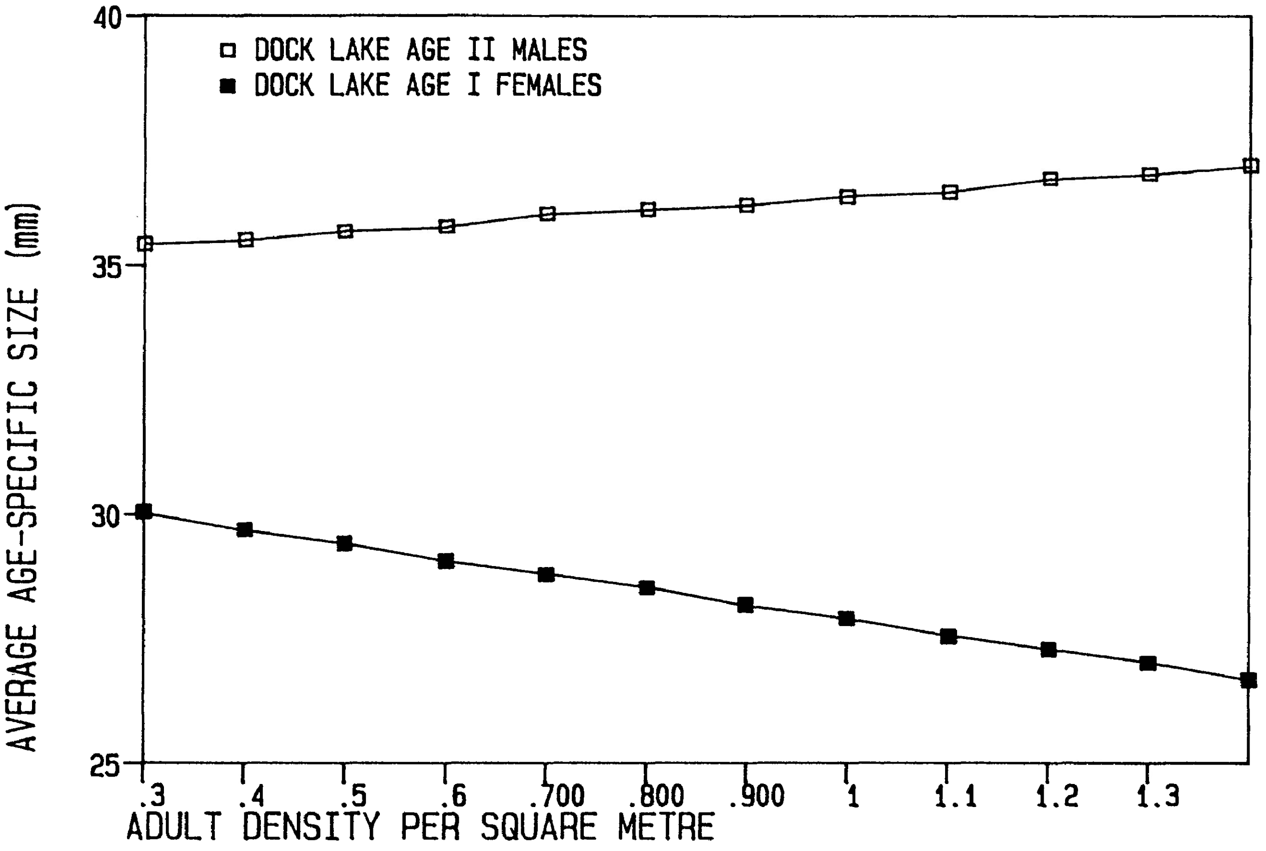
□ SHALLOW LAKE MALES
■ SHALLOW LAKE FEMALES
AVERAGE SIZE OF YOY (mm)
20
19
18
17
16
15
14
13
12
11
10
.9
1
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
TOTAL POPULATION DENSITY PER SQUARE METRE

Figure 4. Relationship between YOY density and YOY size in Shallow Lake 1976 to 1985. Linear regression lines, male: $Y=0.00125X+10.17349$, $R2=0.89$ ($P<0.00008$); female: $Y=0.00121X+10.16435$, $R2=0.65$ ($P<0.005$), for relationship between young-of-year size (Y) and absolute density of young-of-year (X).



□ SHALLOW LAKE MALES
■ SHALLOW LAKE FEMALES
AVERAGE SIZE OF YOY (mm)
ABSOLUTE DENSITY OF YOY
10
11
12
13
14
15
16
17
18
19
20
1000
2000
3000
4000
5000
6000
7000

Figure 5. Relationship between size of age II male, age I female crayfish and adult density per m2 in Dock Lake 1976 to 1985. Linear regression lines, age II male crayfish: $\ln Y=0.04071X+3.55375$, $R2=0.53$ ($P<0.009$); age I female crayfish: $\ln Y=-0.10366X+3.43139$, $R2=0.62$ ($P<0.004$), for relationship between logarithmically transformed (Napierian logarithm) age- and sex-specific size (Y) and adult density per m2 (X).



□ DOCK LAKE AGE II MALES
■ DOCK LAKE AGE I FEMALES
AVERAGE AGE-SPECIFIC SIZE (mm)
40
35
30
25
.3
.4
.5
.6
.700
.800
.900
1
1.1
1.2
1.3
ADULT DENSITY PER SQUARE METRE

Table 2. Age- and sex-specific size (mm) and coefficient of variation (C.V.%) of crayfish in Shallow Lake for 1976 to 1985 cohorts.

TABLE 2. Age- and sex-specific size (mm) and coefficient of variation (C.V.%) of crayfish in Shallow Lake for 1976 to 1985 cohorts.

Year-		YOY			I			II			III	
Class	Size (mm)	C.V. (%)[1]	Sample Size	Size (mm)	C.V. (%)	Sample Size	Size (mm)	C.V. (%)	Sample Size	Size (mm)	C.V. (%)	Sample Size
Male												
1976	19.9	11.70	236	32.4	6.88	497	37.5	2.57	225	43.8	1.44	10
1977	17.9	9.17	194	31.4	7.40	667	37.3	5.82	209	45.7	1.29	3
1978	15.1	9.33	18	30.8	6.96	460	39.1	5.53	387	43.9	1.83	20
1979	12.9	15.64	74	33.6	5.70	747	36.7	5.84	568	44.4	1.95	13
1980	13.4	13.25	77	31.5	4.76	461	39.7	3.74	346	42.6	3.93	143
1981	14.4	15.84	128	33.1	8.97	449	38.7	2.72	307	45.6	1.75	22
1982	11.7	12.79	107	31.4	9.11	484	39.6	5.27	679	44.4	3.13	86
1983	11.5	16.44	56	32.3	7.40	397	38.1	5.25	818			
1984	12.4	14.08	119	29.9	8.51	1014						
1985	11.6	13.76	110									
Female												
1976	19.1	11.83	137	28.3	5.56	110	34.2	3.78	116	39.4	2.85	15
1977	17.9	12.96	203	28.7	8.94	458	33.5	4.71	127	41.6	1.73	9
1978	15.4	8.07	15	28.3	7.89	222	36.6	3.94	123	41.8	1.07	5
1979	12.6	14.66	91	31.3	6.48	508	35.8	4.75	171	39.9	2.76	21
1980	13.0	14.91	92	30.4	6.21	442	34.4	5.52	251	37.8	4.57	152
1981	13.6	15.53	129	28.4	5.44	197	33.4	3.33	153	40.2	3.17	45
1982	11.4	14.01	133	28.2	7.45	306	34.0	6.32	382	41.3	2.99	21
1983	11.1	21.04	61	28.5	5.10	147	35.8	4.56	267			
1984	12.2	17.15	156	28.8	10.56	923						
1985	11.2	14.40	123									

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[1] Coefficient of variation = standard deviation/mean x 100%

Mean Growth Rate and Size in Relation to Population Density

Any density-dependent growth component should be manifested as a differential age-/sex-specific growth rate at varying population density. Size of male and female YOY in both lakes is negatively related to adult density.$m^{2.-1}$ (Fig. 2). In contrast the size of Shallow Lake YOY is positively related to total density.$m^{2.-1}$ (adult density + YOY density) (Fig. 3). Shallow Lake male and female YOY size is also positively related to absolute YOY density (Fig. 4). Therefore not only is the size of YOY density-dependent on adult density in Shallow Lake but YOY size is also indicative of year-class strength. In contrast no similar trend was evident in Dock Lake despite the increase in adult density over the same time period. Exploitation caused a breakdown in the mechanism controlling correlative year-class strength and growth. As a result YOY size is not predicted by YOY density in Dock Lake.

The mean length of Dock Lake age II males is positively related to adult density.$m^{2.-1}$ but the size of Dock Lake age I females is negatively related (Fig. 5). These females form the largest fraction of the reproductive segment of the population. Thus as population density in the exploited lake increases, sexually mature age II males grow larger while age I females decrease in size; as a result potential egg production decreases.

The main effect of cohort density is on the mean size of YOY and their growth rate during the egg-to-YOY stage in Shallow Lake. However cohort densities have no effect on mean sizes and growth rates for the rest of the cohort life span (Table 2). Dock Lake cohorts are similar (Table 3). As a result density-dependent

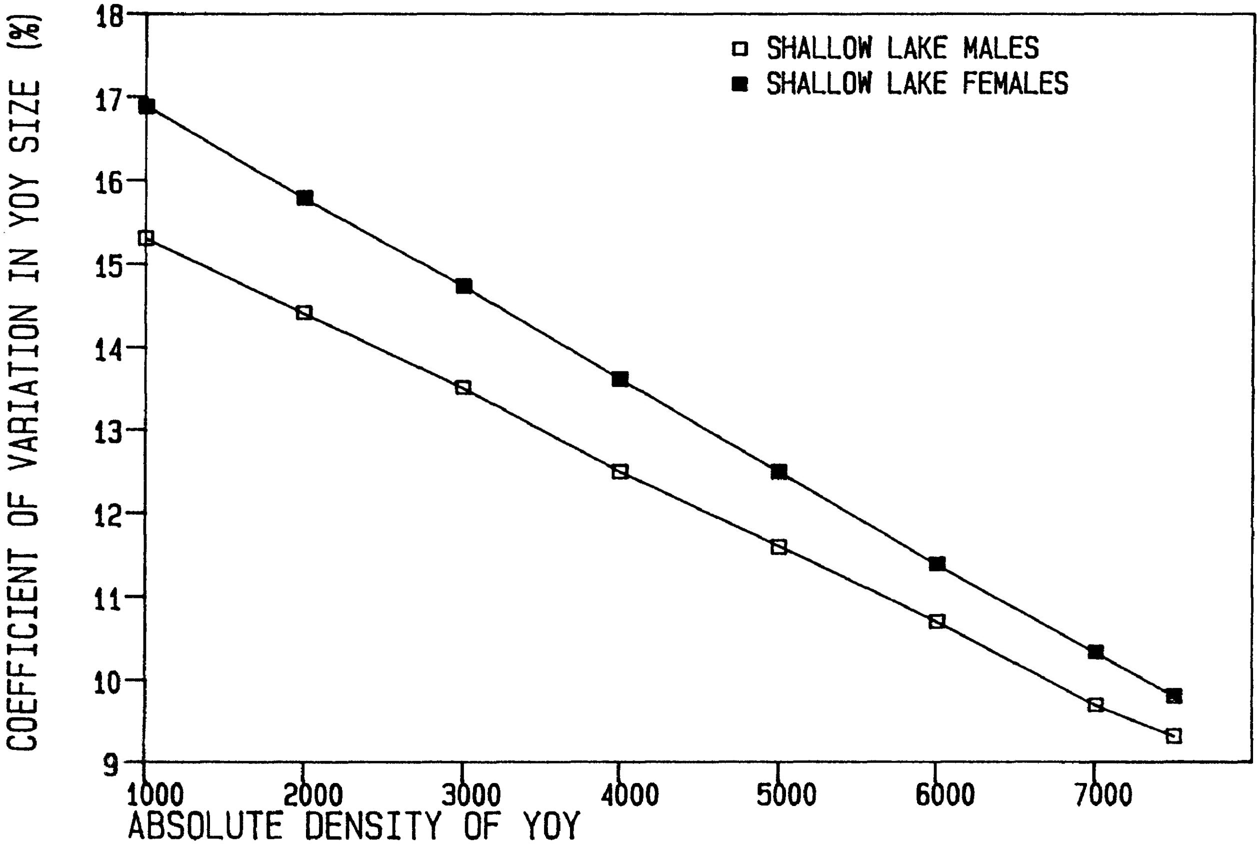
Table 3. Age- and sex-specific size (mm) and coefficient of variation (C.V.%) of crayfish in Dock Lake for 1976 to 1985 cohorts.

TABLE 3. Age- and sex-specific size (mm) and coefficient of variation (C.V.%) of crayfish in Dock Lake for 1976 to 1985 cohorts.

Year-Class	YOY			I			II			III		
	Size (mm)	C.V. (%)[1]	Sample Size	Size (mm)	C.V. (%)	Sample Size	Size (mm)	C.V. (%)	Sample Size	Size (mm)	C.V. (%)	Sample Size
Male												
1976	17.3	14.13	223	31.8	6.04	455	37.4	4.91	417	44.8	3.10	8
1977	18.4	12.47	135	31.2	6.59	660	37.8	3.67	159	43.0	2.53	19
1978	11.1	13.46	84	29.4	5.57	269	37.8	4.24	212	41.2	3.15	52
1979	12.5	14.90	70	32.4	6.38	428	36.4	3.13	204	42.6	1.74	39
1980	13.8	13.72	54	31.9	5.22	230	38.5	3.15	407	43.1	1.96	59
1981	14.3	16.94	238	32.1	7.64	1672	38.4	4.56	625	44.0	3.02	40
1982	11.3	14.43	131	31.1	7.74	2311	39.0	4.16	537	43.9	2.34	47
1983	10.9	14.01	206	31.6	8.53	2020	36.8	5.92	968			
1984	11.6	16.78	164	29.4	7.64	3149						
1985	11.8	16.41	158									
Female												
1976	16.4	12.16	167	29.5	7.61	197	34.0	5.23	220	38.2	2.80	17
1977	16.9	11.45	74	28.4	7.67	392	33.5	9.11	149	42.0	2.43	3
1978	10.6	16.74	90	28.1	12.50	197	35.5	4.12	127	39.4	1.62	14
1979	11.9	18.06	71	30.3	6.36	372	35.3	3.41	120	41.5	2.95	26
1980	12.5	13.05	47	30.4	6.33	258	34.8	5.18	508	41.2	3.32	73
1981	13.5	17.24	215	29.4	7.55	1007	36.6	3.88	411	40.0	3.65	66
1982	10.8	13.06	168	29.7	8.60	1811	34.0	4.65	508	40.1	2.68	29
1983	10.3	16.16	210	28.6	6.57	982	33.1	5.72	995			
1984	11.1	16.43	172	27.2	8.32	2051						
1985	11.7	14.06	141									

[1] Coefficient of variation = standard deviation/mean x 100%

Figure 6. Relationship between coefficient of variation (%) of YOY size and YOY density in Shallow Lake 1976 to 1985. Linear regression lines, male: $Y=-0.00093X+16.24466$, $R2=0.56$ ($P<0.02$); female: $Y=-0.00109X+17.96197$, $R2=0.34$ ($P<0.05$), for relationship between young-of-year size variability (Y) and absoulte density of young-of-year (X).



□ SHALLOW LAKE MALES
■ SHALLOW LAKE FEMALES
COEFFICIENT OF VARIATION IN YOY SIZE (%)
18
17
16
15
14
13
12
11
10
9
1000
2000
3000
4000
5000
6000
7000
ABSOLUTE DENSITY OF YOY

regulation of growth rates or sizes during the life span of a cohort is independent of initial YOY density (i.e., size of the year-class).

Individual Size Variation in Relation to Population Density

Individual size varies as the coefficient of variation (%), exponentially decreases from YOY to age III (Tables 2 and 3). Though males show no significant difference Shallow Lake females are more variable in size than Dock Lake females (Tables 2 and 3).

Size variation of individual male and female YOY in Shallow Lake is density-dependent. It is inversely related to YOY absolute density (Fig. 6). However older age groups are not. Thus following the initial density-dependent effect on YOY in Shallow Lake variation in size of older age groups regularly declines throughout the remainder of the life cycle. The exploited crayfish in Dock Lake, though uneffected by density-dependent mechanisms, shows a similar pattern in size variation throughout the life cycle. The exponential decrease in size variation with age is thus common to both populations and not altered by exploitation.

Table 4. Age- and sex-specific instantaneous growth rates (G) for crayfish in Dock and Shallow Lake 1976 to 1985.

TABLE 4. Age- and sex-specific instantaneous growth rates (G) for crayfish in Dock and Shallow Lake 1976 to 1985.

Lake	Age Interval	Sex	Instantaneous Growth Rate (G) Time Interval 1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Shallow	Egg-YOY	M	1.74	1.63	1.46	1.30	1.34	1.41	1.21	1.19	1.26	1.20
		F	1.70	1.63	1.48	1.28	1.31	1.36	1.18	1.15	1.25	1.16
Dock	Egg-YOY	M	1.60	1.66	1.15	1.27	1.37	1.41	1.17	1.14	1.20	1.22
		F	1.54	1.57	1.11	1.22	1.27	1.13	1.13	1.08	1.15	1.21
			1976-1977	1977-1978	1978-1979	1979-1980	1980-1981	1981-1982	1982-1983	1983-1984	1984-1985	
Shallow	YOY-I	M	0.49	0.56	0.71	0.96	0.84	0.83	0.99	1.03	0.88	
		F	0.39	0.47	0.61	0.91	0.89	0.74	0.91	0.94	0.86	
Dock	YOY-I	M	0.61	0.53	0.97	0.95	0.84	0.81	1.01	1.06	0.93	
		F	0.59	0.52	0.97	0.93	0.89	0.78	1.01	1.02	0.90	
Shallow	I-II	M	0.14	0.15	0.17	0.24	0.09	0.23	0.16	0.23	0.16	
		F	0.16	0.19	0.15	0.26	0.13	0.12	0.16	0.19	0.23	
Dock	I-II	M	0.13	0.16	0.19	0.25	0.12	0.19	0.18	0.23	0.15	
		F	0.13	0.14	0.16	0.23	0.15	0.14	0.22	0.14	0.15	
Shallow	II-III	M	0.07	0.12	0.16	0.20	0.12	0.19	0.07	0.16	0.11	
		F	0.14	0.17	0.14	0.22	0.13	0.11	0.09	0.18	0.19	
Dock	II-III	M	0.12	0.20	0.18	0.13	0.09	0.16	0.11	0.14	0.12	
		F	0.10	0.15	0.12	0.23	0.10	0.16	0.17	0.09	0.16	

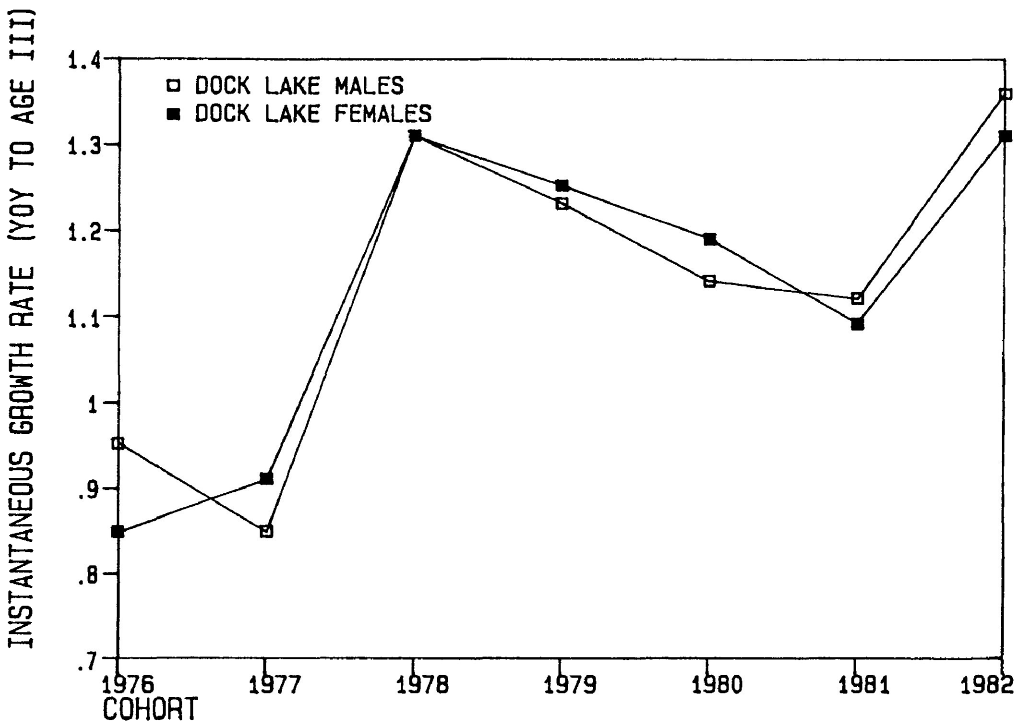
Changes in Mean Growth Rates Related to Exploitation

Annual mean age-specific growth rates were compared between sexes and lakes throughout the decade. No significant difference in growth was evident between Dock and Shallow Lake males between third stage instar and the end of the first summer's growth (YOY) ($P=0.05$) (Table 4). However for females, there was a significant difference. Those in Shallow Lake were larger ($P<0.01$) (Table 4). Also males in both lakes at this stage were larger than females ($P<0.01$) (Tables 2 and 3). Hence during the third stage instar-to-YOY stage males grow at similar mean rates while females are slower growing with Dock Lake females growing the slowest.

At the next life stage (YOY-to-age I) male mean growth rates are similar in both lakes ($P>0.05$) (Table 4). However Dock Lake females grow at a significantly greater rate than Shallow Lake females ($P<0.01$) (Table 4). Shallow Lake males grow at a significantly faster rate than females ($P<0.01$), while Dock Lake males and females have similar rates ($P>0.05$) (Table 4). Hence Dock Lake females grow faster than Shallow Lake females and similar to males in both lakes.

Between the age I-to-age II and age II-to-age III life stage there is no significant difference in mean growth rate between lakes or sexes ($P>0.05$). Therefore a growth response by the exploited population occurred only during the period immediately following independence of the young from the female until they reach age I. In both lakes during the first growing season sexually dimorphic growth produces similar sized YOY males and smaller YOY females, with Dock Lake female YOY being the smallest. During the second growing season (until age I) Shallow

Figure 7. Cohort instantaneous growth from YOY to age III+ of male and female crayfish in Dock and Shallow Lake for 1976 to 1982 cohorts.


INSTANTANEOUS GROWTH RATE (YOY TO AGE III)
□ DOCK LAKE MALES
■ DOCK LAKE FEMALES
1.4
1.3
1.2
1.1
1
.9
.8
.7
1976
1977
1978
1979
1980
1981
1982
COHORT

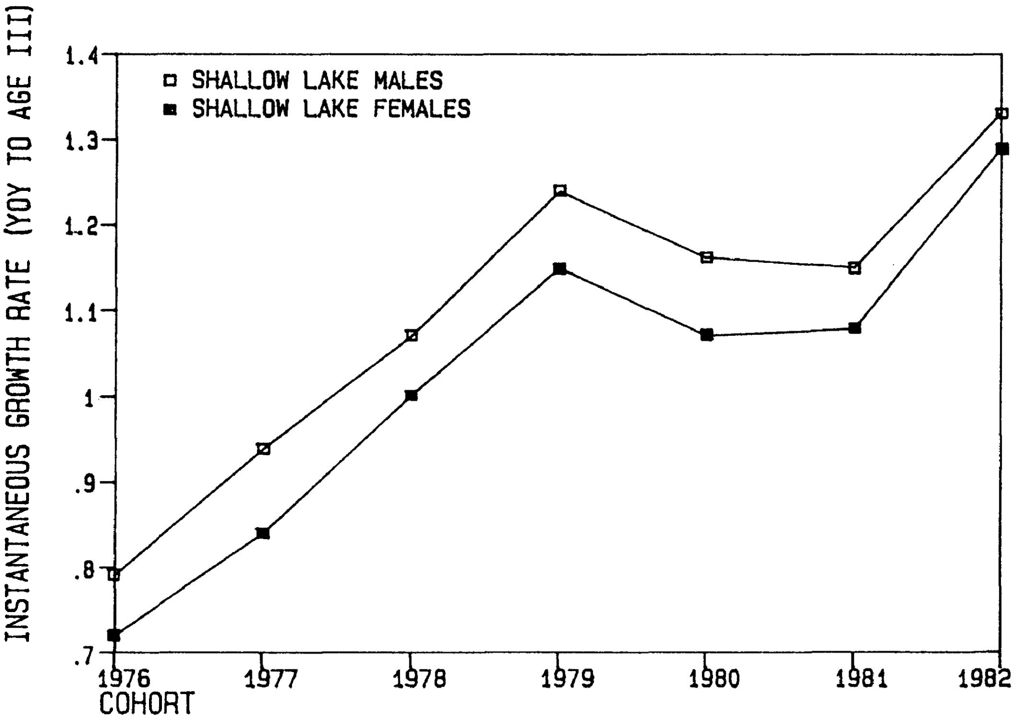

INSTANTANEOUS GROWTH RATE (YOY TO AGE III)
□ SHALLOW LAKE MALES
■ SHALLOW LAKE FEMALES
1.4
1.3
1.2
1.1
1
.9
.8
.7
1976
1977
1978
1979
1980
1981
1982
COHORT

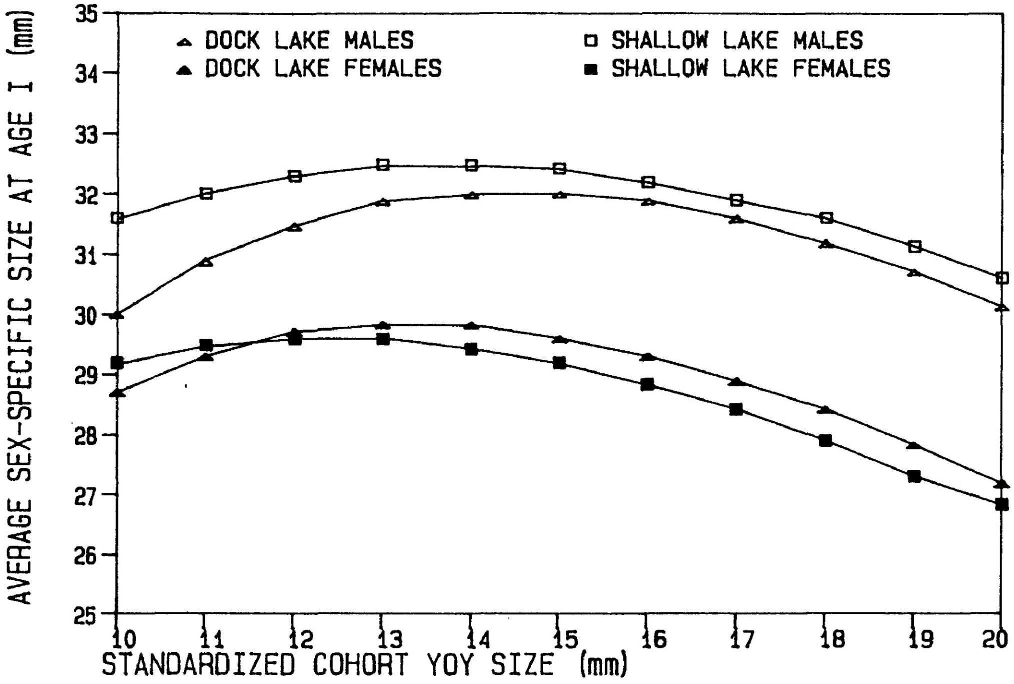
Table 5. Relationships between YOY size and 1976 to 1982 cohort age- and sex-specific instantaneous growth rates (G) in Dock and Shallow Lake crayfish populations.

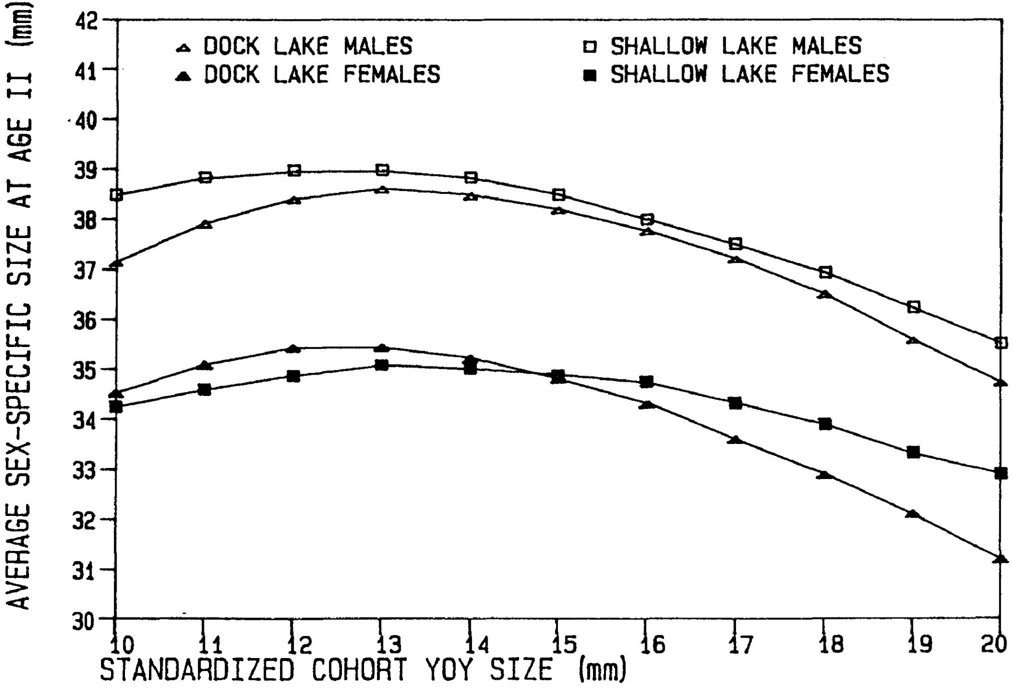
TABLE 5. Relationships between YOY size and 1976 to 1982 cohort age- and sex-specific instantaneous rates (G) in Dock and Shallow Lake crayfish populations.

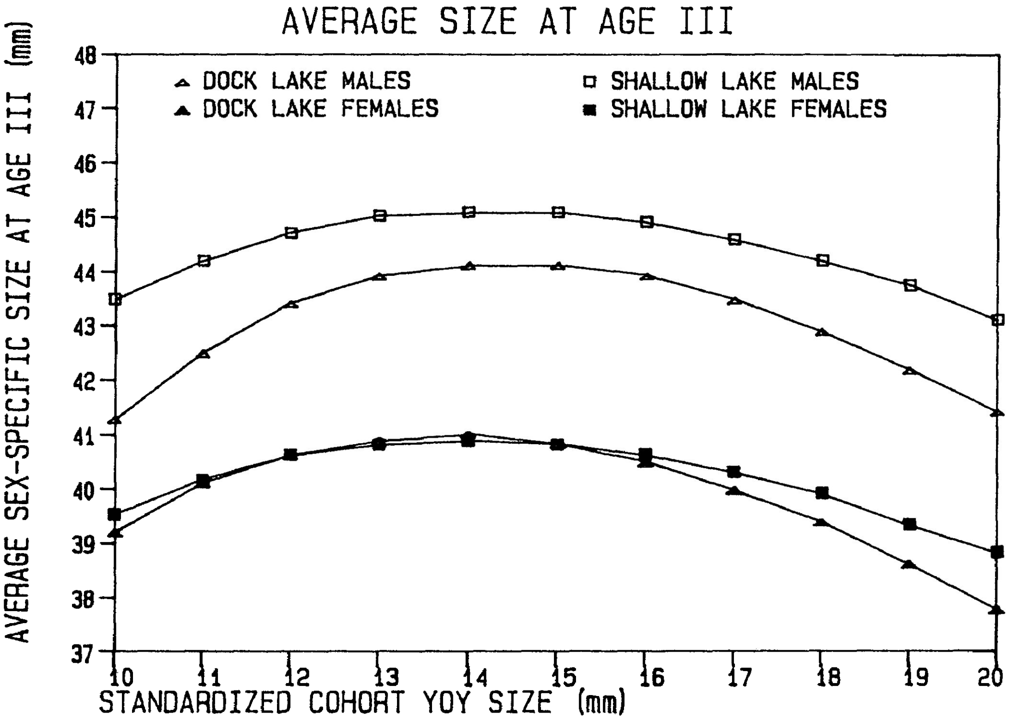
Lake	Sex	Predicted Population Growth Patterns Based on Mean Cohort Age-Specific Growth Rates (G) and Initial Mean Cohort YOY Size (mm)[1]	R^2
Shallow	M	$GI = -0.06470YOY + 1.74321$	0.96
		$GII = -0.07021YOY + 2.00764$	0.98
		$GIII = -0.06249YOY + 2.03712$	0.98
	F	$GI = -0.07266YOY + 1.76625$	0.97
		$GII = -0.06728YOY + 1.85863$	0.97
		$GIII = -0.06517YOY + 1.98035$	0.96
Dock	M	$GI = -0.06459YOY + 1.72783$	0.99
		$GII = -0.07097YOY + 2.00782$	0.98
		$GIII = -0.06484YOY + 2.05134$	0.98
	F	$GI = -0.07477YOY + 1.80192$	0.99
		$GII = -0.07960YOY + 2.03582$	0.99
		$GIII = -0.07284YOY + 2.09359$	0.97

[1] Based on 1976-82 cohorts ($n = 7$); all regressions significant at $p < 0.001$ ($Ho: B = 0$).

Figure 8. Age- and sex-specific dual size equilibria related to initial YOY size of Dock and Shallow Lake 1976 to 1982 cohorts (see Table 5).


AVERAGE SIZE AT AGE I


AVERAGE SIZE AT AGE II


AVERAGE SIZE AT AGE III
DOCK LAKE MALES
DOCK LAKE FEMALES
SHALLOW LAKE MALES
SHALLOW LAKE FEMALES
AVERAGE SEX-SPECIFIC SIZE AT AGE III (mm)
48
47
46
45
44
43
42
41
40
39
38
37
10
11
12
13
14
15
16
17
18
19
20
STANDARDIZED COHORT YOY SIZE (mm)

Lake crayfish still display the sexually dimophic growth pattern. Dock Lake males and females show similar growth rates during the same period. As a result, age I females are of similar size in both lakes.

Even though male growth until age I is comparable between lakes, Shallow Lake age I males are larger in size. This could be the result either of subtle, though statistically similar, growth differences between lakes from third stage instar-to-YOY or the result of size-selective fishing mortality.

Mean cohort growth rates (YOY-to-age III) clearly show the effect of exploitation on the Dock Lake crayfish population (Fig. 7). While Shallow Lake crayfish maintained the sexually dimorphic pattern favouring male growth ($P<0.02$), Dock Lake males and females had the same mean growth rates ($P>0.05$). However since female YOY are smaller than male YOY, males attain a larger age III size.

YOY Regulation of Dual Size Equilibria

Although YOY carapace length can vary by a factor of two, size variation at subsequent ages is much reduced (Tables 2 and 3). The annual mean growth rate from YOY-to-: age I, age II and age III of individual cohorts (1976 to 1982) allows us to predict potential population size curves (Table 5). Standardizing YOY sizes allows comparison between lakes and sexes. All three age classes exhibit dual size equilibria; the same mean size of age I, age II or age III crayfish can result from two different sized YOY. The age-specific size obtained by a cohort throughout it's life span is determined by the initial size of YOY (Fig. 8). The relationships appear similar between the lakes, although the Dock Lake female curves skew towards the smaller YOY sizes, while Shallow Lake males are larger than Dock Lake males. Dock Lake females are larger than Shallow Lake females at age I and age II. This is true for all cohorts with YOY between 10 and 15 mm in size. Therefore although Shallow Lake female third stage instar-to-YOY growth is greater than Dock Lake's, the resulting mean size of Dock Lake's egg producing age I and age II females is larger.

DISCUSSION

Dock Lake crayfish responded to exploitation through altering their age- and sex-specific growth patterns. The size of sexually mature males, in terms of weight-per-unit-length, declined between 1976 and 1984-85 (Table 1). However because there is insufficient time trend data and a lack of comparable control lake data, this conclusion may be somewhat presumptive. Changes in mean age- and sex-specific growth rates reveal a subtle growth response. Though male age-specific growth rates are similar between lakes, Dock Lake males never attain the same size as Shallow Lake males. The slight difference in third stage instar-to-YOY growth cannot account for this size difference. This could be the result of active selection by the fishery for the faster growing males.

Exploitation increased the growth of YOY-to-age I females (Table 4). In both lakes the cohorts produced since 1978 began as YOY less than 15 mm in size. Thus Dock Lake females reached larger size at subsequent ages (Figures 8). The initial slow growth of Dock Lake females was more than compensated during later growth periods. Therefore the exploitation of Dock Lake crayfish has produced separate and distinct male and female responses. While male growth rates remained unchanged, size-selective fishing mortality probably reduced male size upon recruitment to the exploitable stock at age I. Meanwhile juvenile female growth increased, producing larger sized crayfish at age I and age II. This female response occurred during sexual maturity (size at the onset of sexual maturity = 24.3 mm carapace length, standard deviation = 1.00) when females reach 72.9% (standard deviation = 2.93) of their final size (age III+). Upon reaching age I the age- and sex-specific growth rates are similar between lakes. As a result any growth response to exploitation is short-lived influencing only immature females.

Exploitation has not altered the pattern of variation in individual size. In both lakes size variation exponentially decreases with age (Tables 2 and 3). However the potential causal mechanism, whether individual variation in growth patterns or size-selective mortality, both of which in turn could control size variation, remains unknown. Shallow Lake YOY size variation appears related to YOY density and adult density, (Fig. 2, 3, 4 and 6). Although Dock Lake YOY display the same patterns in size variation with adult density, the YOY density relationship does not hold. Therefore although YOY size variation and YOY density are mathematically dependent this is not a biological cause and effect relationship. More likely the decrease in YOY size variation with increasing YOY size and density relates to a negative biotic feedback with adult crayfish density in Shallow Lake. Shallow Lake YOY growth parameters are indicators of food related stresses acting upon the population. The decrease in size variation with increasing YOY growth and YOY density is apparently the result of density-dependent growth-mortality interactions, both within and between life stages. In Dock Lake exploitation disrupts this mechanism.

Regardless of individual size variation, it is the mean YOY size that controls the average size of later cohort age-classes (Fig. 8). Thus the initial YOY size of a cohort acts as a growth regulating factor relative to initial density-dependent changes (Fig. 2). This programmed growth pattern occurs throughout the whole life history and apparently is insensitive to environmental change. Since exploitation hasn't disrupted the functional growth pattern in Dock Lake, dual size equilibria exist in both lakes with YOY size/growth regulated by adult density. As adult density increases, Dock Lake YOY are comparatively larger in size than those in Shallow Lake (Fig. 2). However this difference isn't manifested throughout the life span since cohorts irregardless of initial YOY size achieve the same age-specific size. The effect of a decrease in growth rate with an increase in YOY size results in crayfish achieving their maximal age-specific size potential at intermediate YOY size (Table 4). Therefore in Dock Lake exploitation acts as a positive feedback on YOY size and growth, especially as adult density increases. However the variable growth rates which produce similar sized crayfish obscure cause-and-effect relationships between the exploited and control lake populations. Apparently life stage growth rates are more closely correlated with initial YOY size rather than with chronological age.

Divergence in YOY growth patterns could be caused by: (1) the annual environmental cycle, namely temperature and food availability (cf., Momot 1984) and/or (2) changes in population density. Other field studies of crayfish growth conclude that temporal variation in size are caused by changes in temperature regimes (Pratten 1980; France 1985). In contrast, we maintain that changes in mean cohort age-specific sizes are mediated through adjustments in YOY growth rates. This adjustment is the consequence of a population density-dependent feedback occurring during the earliest life stage. Changes in temperature input during the growing season (growing-degree-days $>15^{o}$C (Aiken 1969; Pratten 1980)) varied three-fold during the decade of study, yet did not explain the variability in YOY growth (Fig. 2). Considering both the short life span and limited breeding period of this species, only an intrinsic density feedback mechanism regulating growth rather than stochastic variation in climate could produce the homeostatic annual turnover ratios (P/B) observed in this and other northern populations of **Orconectes virilis** (Momot and Gowing 1977a; Momot 1984; Momot 1986).

YOY growth may be regulated by intraspecific competition for a temporary food supply or dissynchrony between hatching and a suitable food source. We hypothesize that this relative food shortage is exacerbated by a seasonal food habit overlap between adults and YOY. The exact food source could be zooplankton, benthos, benthic algae or phytoplankton. Primary productivity by phytoplankton is controlled by phosphorous availability in marl lakes (Wetzel 1983). Perhaps zooplankton or phytoplankton serve as an early food source. According to Thomas (1978) mouthpart setae morphology may define obligate and opportunistic feeding stages in crayfish. Filter feeding is thought to be the dominant mode of food collection in fourth stage instar **Austropotamobius pallipes** Lereboullet while adults may be opportunistic filter feeders (Thomas 1978). Free-living YOY and adult **Orconectes propinquus** (Girard) and **Cambarus robustus** Girard did remove algae from suspension in laboratory experiments (Budd et al. 1979). Perhaps YOY **O. virilis** make use of filter feeding during early instars. Momot et al. (1978) examining the food habits of YOY **O. virilis** in Michigan marl lakes found all stomachs contained detritus, defined as: "amorphous organic and inorganic material including aggregations of marl, nonfilamentous algae and diatoms". Research on seasonal and age-specific food habits of these YOY and adult crayfish is necessary to clarify this problem.

The effect of exploitation on sexually dimorphic growth responses has significance for crayfish management. Accurate forecasting of future size potential and adult density may be possible from easily obtained YOY point samples. If maximizing individual size is the goal, then reducing adult densities below 0.30-0.40 adults.$m^{2.-1}$ would produce the largest males. Reducing adult densities below 0.50-0.75.$m^{2.-1}$ would produce the largest females. Exploitation normally decreases the average size of males while increasing female size. Since harvesting of this species appears to be male size selective (Threinen 1958; Abrahamsson 1966; Momot and Gowing 1977b), their average size will decrease with increasing levels of exploitation. However, exploitation rates could be adjusted to produce an optimal growth and density combination. In unexploited populations the relationship between YOY size and YOY density could prove useful for assessing possible surplus production. This surplus could be used for tranfer stocking or for culture purposes without inducing detrimental effects on the crayfish population.

Individual size variation is strongly regulated within a narrow range. The size of YOY is density-dependent on adult population. Cohort age-specific growth rates depend on YOY size even when cohorts grow under different and varying adult density conditions (i.e., YOY size is the major determinant of growth rates in crayfish). This produces regularity in the growth pattern. Consequently, growth functions are determined and fixed early in the life cycle and initial size variability is regulated by nutritional condition. Crayfish apparently are able to maintain a minimum genetically determined growth rate resulting in size specificity during the life cycle. Exploitation increases the female YOY-to-age I growth rate. This results in larger age I and age II females which in turn stimulates an increase in individual (per capita) fecundity (Morgan 1987).

The response in juvenile female growth occurred after the 1978 harvest. At a nominal effort of 1350 trap-days (150 traps for 9 days) the harvest removed 35% of Dock Lake's population (42% of the males and 28% of the females). During this period male YOY-to-age I growth also increased in Dock Lake. From 1978 to 1979 juvenile growth rates in the exploited population nearly doubled. Shallow Lake YOY-to-age I growth rates linearly increased in a step-wise manner from 1976 until 1980. Since 1980 both lakes have had similar juvenile growth rates.

The growth response of northern crayfish populations to exploitation occurs from the juvenile to mature life stage. Harvests of one-third of the exploitable stock cause the subtle growth rate increase, however detection of this response without a suitable control population would be difficult if not impossible. The ability to manage crayfish stocks based on growth responses using standard relationships or indices would be severely limited because of the age- and sex-specific nature of the response, and the labile YOY size/growth rate interaction producing dual size equilibrium.

Although exploitation levels have increased forty-fold since 1977, we have been unable to detect growth overfishing. The limited growth response of immature female crayfish has resulted in increased per capita fecundity and YOY production in Dock Lake (Morgan 1987). As stated in Momot (1984) severe levels of exploitation could predispose northern crayfish stocks to recruitment overfishing without first manifesting symptoms of growth overfishing. This study appears to confirm that possibility. A possible alternative for growth assessment of these exploited stocks would be variation in prereproductive female growth rates. It appears that growth overfishing in crayfish, and possibly other benthic crustaceans, may be less important than recruitment overfishing because of their limited response as related to their determinate growth pattern.

Growth studies of crayfish frequently concentrate on changes in individual size variation or individual growth patterns. Our investigation of long-term responses has shown that such an emphasis can be misleading if it ignores variation in mean YOY size and the effect of fixed growth patterns, because the former is not a stable characteristic of crayfish populations. Individual YOY size varied considerably between year-classes in both crayfish populations and was density-dependent. Exploitation failed to change the overall pattern in size variation or growth in Dock Lake. The degree of relative mean size variation in each year-class was established during the first few months of the life cycle and then remained fixed (i.e., constant growth pattern) throughout the life span. Thus annual or short-term studies of crayfish growth are actually measuring the lag response of the initial determination of the fixed growth pattern. The result is that the present size structure of any crayfish population is the sum of past density-dependent lagged growth patterns and is unrelated to abiotic/biotic conditions at the time of measurement.

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MORTALITY

Morgan, G.E. & W.T. Momot. 1987. Changes in mortality patterns of the crayfish **Orconectes virilis** related to exploitative pressure. In preparation.

ABSTRACT

Seasonal crayfish mortality in the exploited population of Dock Lake varied from that in the control population of Shallow Lake. During spring Shallow Lake female mortality is associated with intraspecific aggression while that in Dock Lake is moult related. Summer mortality in both lakes correlates with the annual moult. Shallow Lake crayfish also have a higher incidence of porcelain disease. Because of the intense 1985 harvest in Dock Lake very few adult crayfish died of natural causes. Mortality was higher in Shallow Lake than in Dock Lake during the spring and summer. Male mortality rate does not differ from that of females during the summer in either lake. During harvest mortality was similar between the sexes in Dock Lake. Dock Lake females suffered higher mortality during spring spawning than in either summer or during harvest. Mortality in males from Dock Lake and Shallow Lake was related to poor physiological condition.

All crayfish examined were infected by the internal parasite **Psorospermium haeckeli** Hilgendorf. This is the first record in the genus **Orconectes** and on the North American continent. Of 5558 crayfish examined during the 1985 harvest, one gynandromorph was found.

Abrahamsson's index of population stress failed to detect differences between relative densities or absolute densities. Exploitation alters age- and sex-specific annual mortality rates. During the egg-to-young-of-year (YOY) life stage, Shallow Lake crayfish have higher mortality rates than Dock Lake crayfish. Dock Lake females suffer higher mortality during the YOY-to-age I life stage compared to either males or either sex in the control population. However during the age I-to-age II life stage the mortality of Dock Lake males becomes greater than that of either females or Shallow Lake crayfish. This increased mortality occurs during the life stage at which female and male sexual maturity is attained.

Key-factor analysis revealed that mortality from egg-to-YOY regulates population growth of Shallow Lake crayfish and males in Dock Lake. Dock Lake female density is controlled by mortality from egg-to-age I. Shallow Lake crayfish exhibit strong density dependent mortality from egg-to-YOY and YOY-to-age I. As a result one-third to over one-half of the exploitable stock (age I+) can be harvested annually without significantly effecting recruitment. Population declines occur when total annual mortality of the exploitable stock exceeds 75%.

INTRODUCTION

Exploitation of the crayfish, **Orconectes virilis** (Hagen), inhabiting Michigan marl lakes modified their age- and sex-specific mortality rates (Momot and Gowing 1977a, b and c). These responses, together with adjustments in age-specific fecundity, regulated population densities and accounted for their resilience to exploitation. However, the before-and-after experimental design used in the Michigan study was confounded by changing environmental gradients which confused cause-and-effect relationships (Momot and Gowing 1977c).

The present study avoids this problem by deliberately over-exploiting the crayfish population in Dock Lake while monitoring the unexploited population of nearby Shallow Lake. We hoped this control-treatment experimental design would correct for the possible confounding of variables due to spatial and temporal relationships (Green 1979). In this report we examine variation in yearly mortality rates and seasonal mortality factors effecting both populations. The role of annual mortality changes in controlling population fluctuations was investigated with `key factor analysis' (Varley, Gradwell and Hassell 1973).

STUDY AREA AND METHODS

Since 1977, we have exploited crayfish in Dock Lake with modified minnow traps. Nominal effort increased forty-fold, from 150 to 6000 trap-days during the nine years. A trap-day is one minnow trap fished 24 hours. For comparision the population in Shallow Lake has served as a simultaneously monitored control. The study area's physical-chemical properties and general methods are described in Momot (1978) and Morgan (1987); only additional methods specific to this portion of the study are described here.

Following sequential estimates of the Dock Lake population, we exploited the crayfish by approximating the Type I fishery of Ricker (1975, pg. 10). This allows for natural and fishing mortality to be placed in separate periods. By carefully timing sampling intervals in both lakes we analysed seasonal mortality factors. Dock and Shallow Lake populations were sampled using the same sampling intensity (number of $traps.m^{-1}$ of shoreline) and frequency (the same number of sample days). The sampling methods were size-selective for crayfish age I and older. During the 1985 field season, all dead crayfish were collected and examined in the laboratory. Crayfish were measured from the tip of the rostrum to the posteriomedial edge of the carapace to the nearest 0.05 mm using vernier calipers. Wet weights were measured to the nearest 0.001 gram using a digital balance.

Dead crayfish were necropsied for: (1) moult condition, (2) morphological deformities or anomalies, (3) damaged (i.e., lost or regenerating) chelipeds and pereiopods, (4) presence of porcelain disease (Theolania sp.) and (5) presence of Psorospermium haeckeli Hilgendorf.

During intermoult, following the male maturity moult to form I, a random sample of the populations in both lakes was inspected for contingent mutilations of the chelipeds and pereiopods. Abrahamsson (1966) considered the frequency of appearance of damaged appendages to indirectly measure stress induced by high population density. By comparing this stress index between control and exploited lakes we hoped to be able to indicate differences in relative and absolute density.

Key-factor analysis, using life table data for the 1976 to 1982 cohorts, examined sequential mortality factors between successive life stages (Varley, Gradwell and Hassell 1973). The total mortality rate (K) corresponds to half the total egg production which produced the cohort. The sex ratio was assumed to be unity at hatching (K = ln(egg production/2)). Mortality was separated into natural and fishing components for Dock Lake. The age III-to-age III+ life stage was not analysed due to autocorrelation between density and mortality rates (i.e., this is the end of the life cycle and all crayfish die during this interval). Possible density-dependent/independent relationships were investigated by intra-life stage comparisons between mortality rate ("loss-rate" = k) and life stage density (logarithmically transformed).

Prevalence of seasonal mortality factors and damage to appendages between lakes and sexes was examined through contingency table analysis (Zar 1974). However during spring (June 26 to July 10) only the females were examined because catching tentatives were unsuccessful for males due to the annual moulting cycle (i.e., form I to form II). Only Dock lake crayfish were sampled during harvest (August 7 to September 2). All of this limited comparisons between sexes and sampling periods. Changes in age- and sex-specific mortality rates were compared using Wilcoxon matched-pairs signed-ranks test (Daniel 1978). Differences in mean size were tested using the student t-test (Sokal and Rohlf 1981). The carapace length (mm) to wet weight

Table 1. Spring mortality sample from Dock and Shallow Lake June 26 to July 10, 1985.

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Lake	Sex	Age	Spring Necropsy Sample (June 26-July 10)				Carapace Length (mm)	Number Sampled Alive
			Moulted	Damaged Legs	Porcelain Disease	Total		
Shallow	M	I	-	1	1	2		
		II	1	1	1	2		
		III	-	1	1	1		
		Total	1	4	3	5	35.9(3.01)[1]	
	F	I	-	11	-	15		
		II	1	13	3	19		
		III	-	7	1	7		
		Total	1	31	4	41	32.3(0.67)	1004
Dock	M	I	3	-	-	3		
		II	6	-	7			
		III	-	-	-	-		
		Total	9		2	10	35.3(1.43)	
	F	I	2	2	1	7		
		II	2	4	-	5		
		III	-	1	-	1		
		Total	4	7	1	13	31.7(1.15)	632

[1] Mean (standard error)

Table 2. Summer mortality sample from Dock and Shallow Lake July 16 to August 6, 1985.

TABLE 2. Summer mortality sample from Dock and Shallow Lakes July 16 to August 6, 1985.

Lake	Sex	Age	Summer Necropsy Sample (July 16-August 6) Moulted	Damaged Legs	Porcelain Disease	Total	Carapace Length (mm)	Number Sampled Alive
Shallow	M	I	19	8	3	19		
		II	14	7	3	14		
		III	6	2	-	8		
		Total	39	17	6	41	34.8(1.04)	1878
	F	I	10	4	4	11		
		II	17	5	5	18		
		III	9	6	1	9		
		Total	36	15	10	38	32.4(0.68)	1175
Dock	M	I	8	2	-	8		
		II	1	-	-	1		
		III	-	-	-	-		
		Total	9	2		9	29.5(1.25)[1]	1630
	F	I	3	3	-	3		
		II	7	2	-	8		
		III	-	-	-	-		
		Total	10	5		11	30.7(0.87)	1189

[1] Mean (standard error)

Table 3. Harvest mortality sample from Dock Lake August 7 to September 2, 1985.

TABLE 3. Harvest mortality sample from Dock Lake August 7 to September 2, 1985.

Lake	Sex	Age	Harvest Necropsy Sample (August 7 - September 2)					Number Sampled Alive
			Moulted	Damaged Legs	Porcelain Disease	Total	Carapace Length (mm)	
Dock	M	I	7	1	1	7		
		II	4	4	-	4		
		III	-	-	-	-		
		Total	11	5	1	11	32.3(1.31)[1]	3273
	F	I	4	2	-	4		
		II	9	4	-	9		
		III	-	-	-	-		
		Total	13	6		13	31.5(1.05)	2261

[1] Mean (standard error)

(gm) power relationships were logarithmically transformed to allow linear regression. Analysis of covariance (Snedcor and Cochran 1967) determined any differences between-sex comparisons and between-lake comparisons.

RESULTS

Seasonal Mortality Patterns

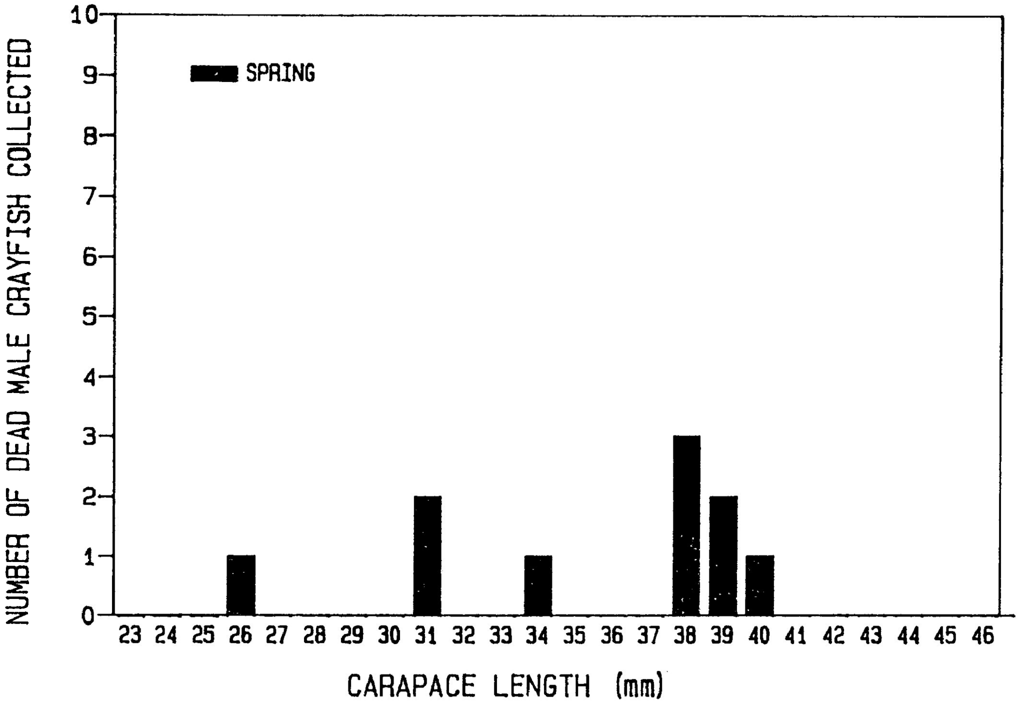
Seasonal age- and sex-specific mortality patterns differed between lakes. Dock Lake age I male mortality was highest during summer and harvest sampling periods (Tables 1, 2 and 3). Age II male mortality occurred primarily during the spring. No age III males were collected. Mortality of age I females in Dock Lake decreased after the spring. Age II female mortality increased from spring until harvest. Only one age III female was examined in Dock Lake.

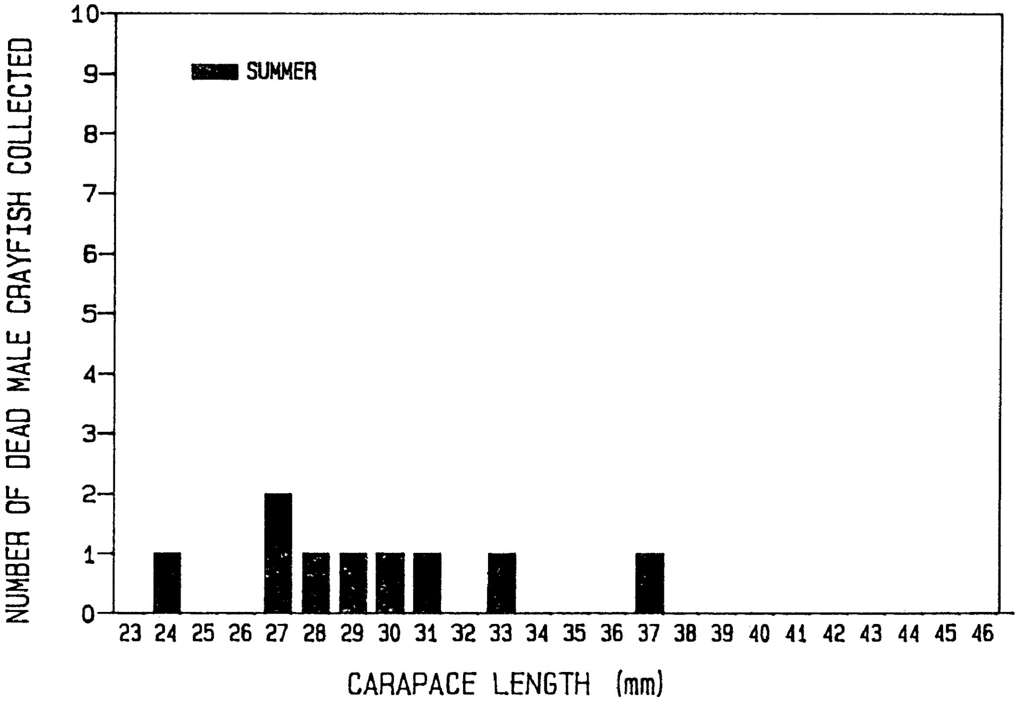
Very few age I, age II and age III dead male crayfish were collected in Shallow Lake during the spring (Tables 1, 2 and 3). Summer mortality of Shallow Lake male crayfish decreased with age. Female mortality increased from age I to age II, then decreased to age III in Shallow Lake. The pattern being similar in both spring and summer collections.

Female mortality was proportionately greater in Shallow Lake than Dock Lake during spring ($P<0.05$) and summer ($P<0.005$) (Tables 1 and 2). Among males summer mortality was higher ($P<0.005$) in Shallow Lake than in Dock Lake (Table 2). There were no differences between male and female mortality during summer in Shallow Lake or summer and harvest in Dock Lake (Tables 2 and 3).

Figure 1. Size frequency of Dock Lake dead male crayfish collected during the spring, summer and harvest sampling periods 1985.

DOCK LAKE MALE CRAYFISH





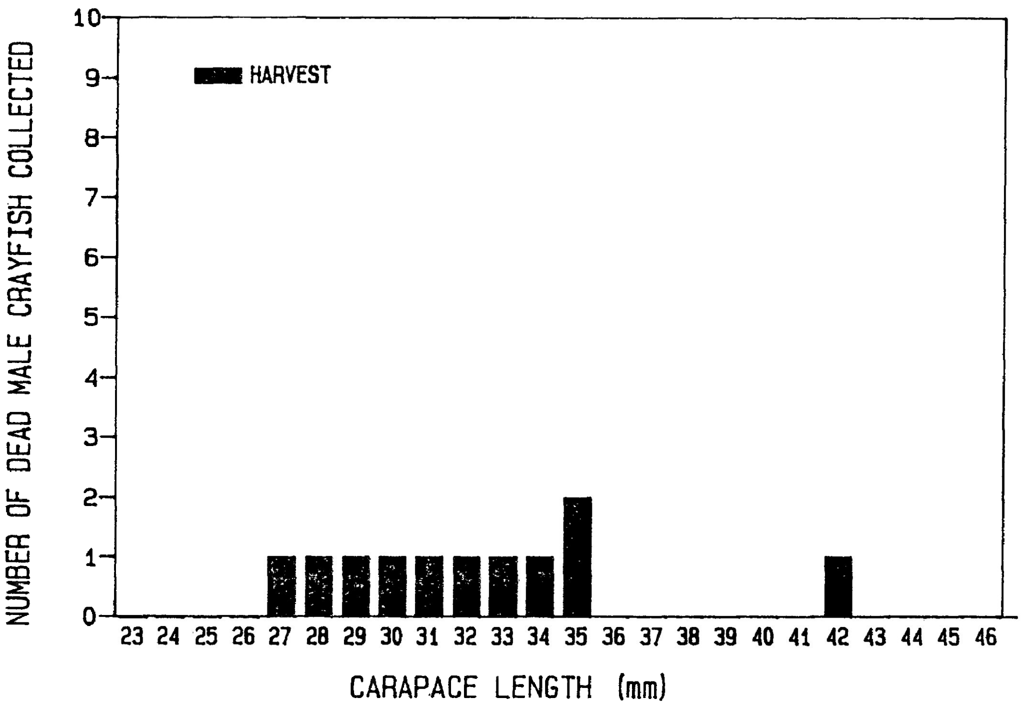
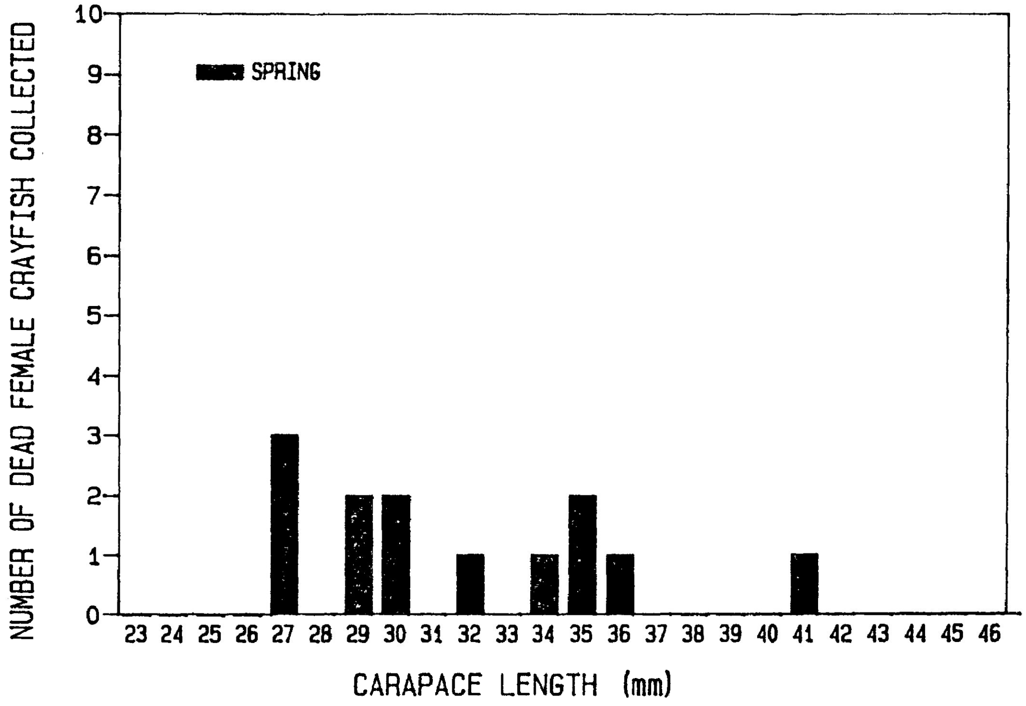
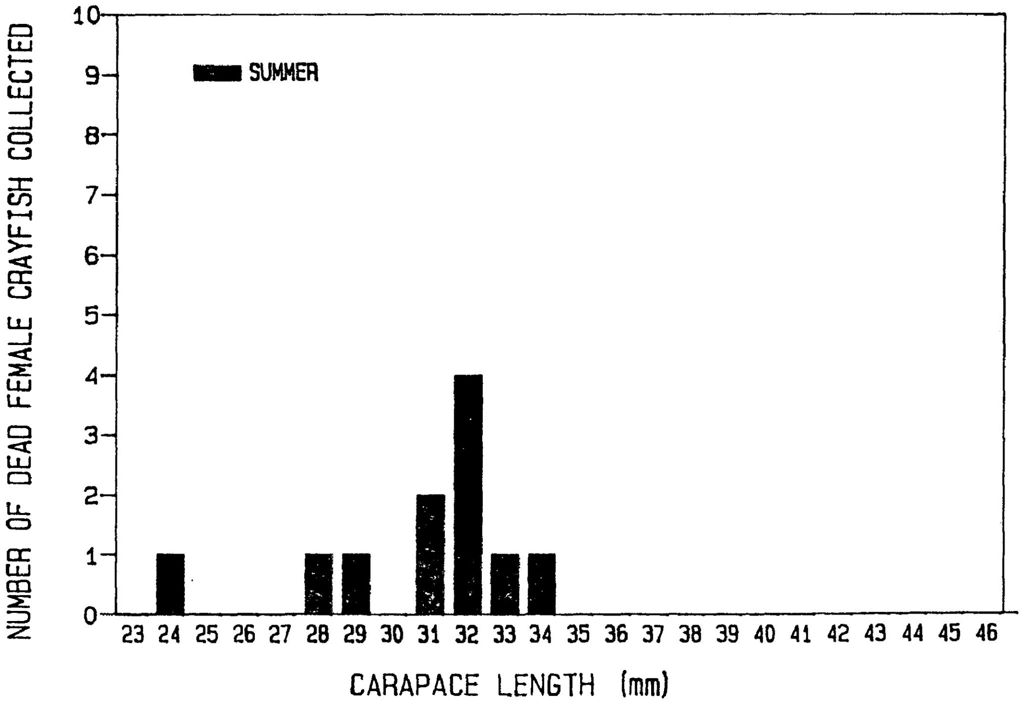

HARVEST
NUMBER OF DEAD MALE CRAYFISH COLLECTED
0
1
2
3
4
5
6
7
8
9
10
23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46
CARAPACE LENGTH (mm)

Figure 2. Size frequency of Dock Lake dead female crayfish collected during the spring, summer and harvest sampling periods 1985.

DOCK LAKE FEMALE CRAYFISH





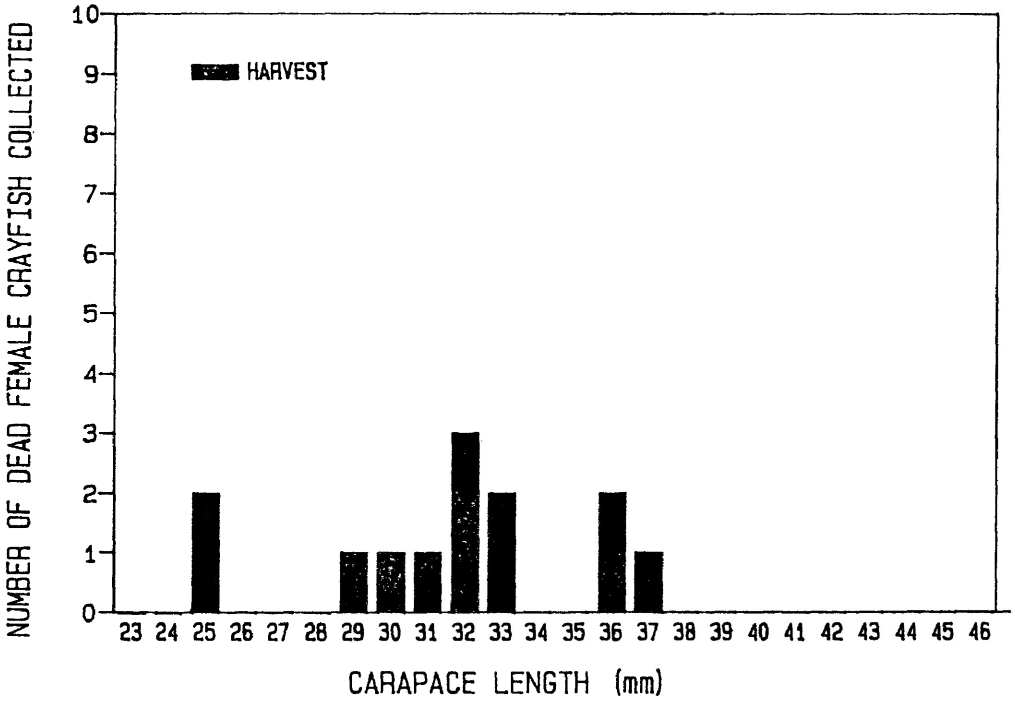

HARVEST
NUMBER OF DEAD FEMALE CRAYFISH COLLECTED
0
1
2
3
4
5
6
7
8
9
10
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
CARAPACE LENGTH (mm)

Figure 3. Size frequency of Shallow Lake dead male crayfish collected during the spring and summer sampling periods 1985.

SHALLOW LAKE MALE CRAYFISH

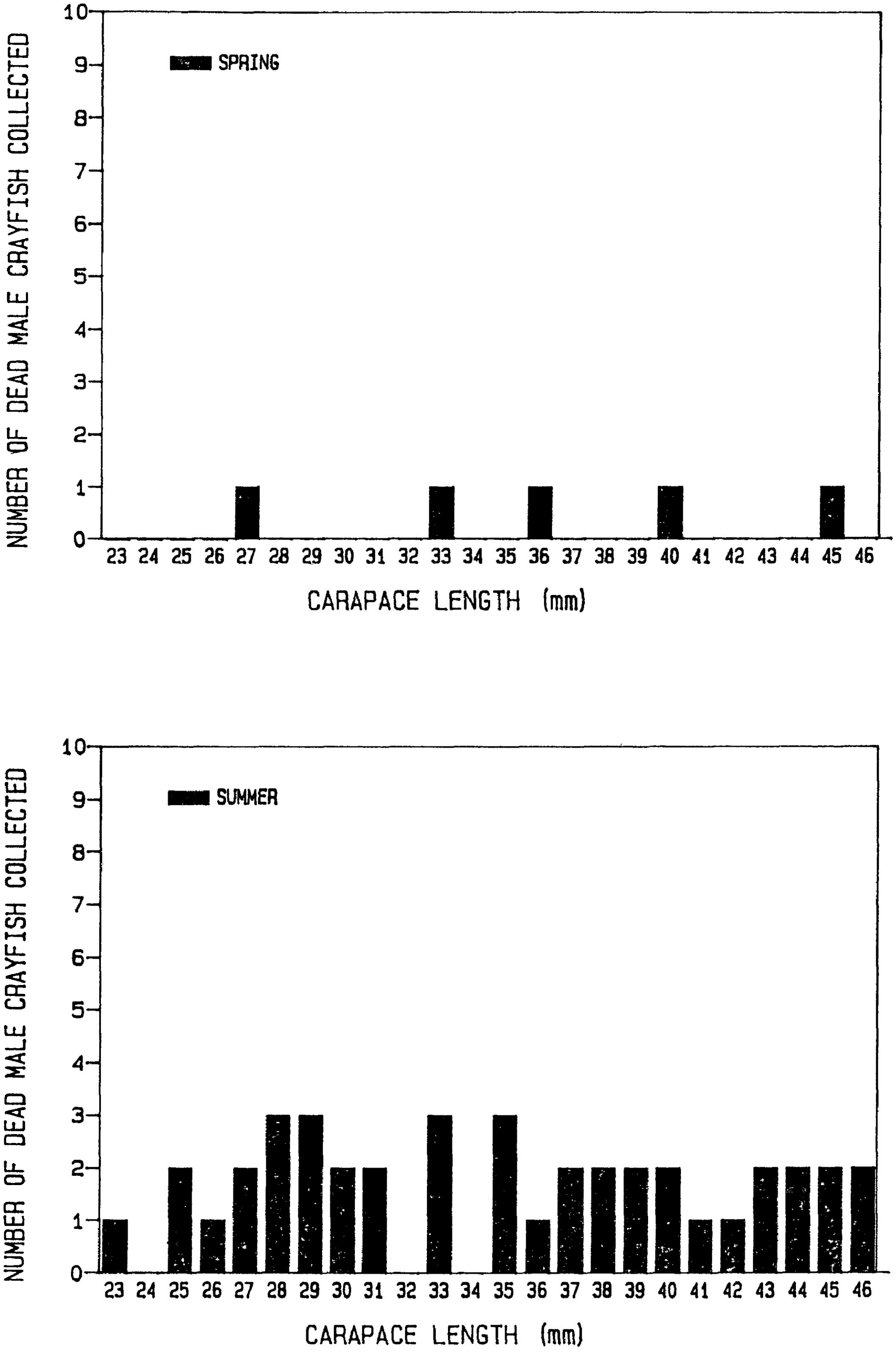
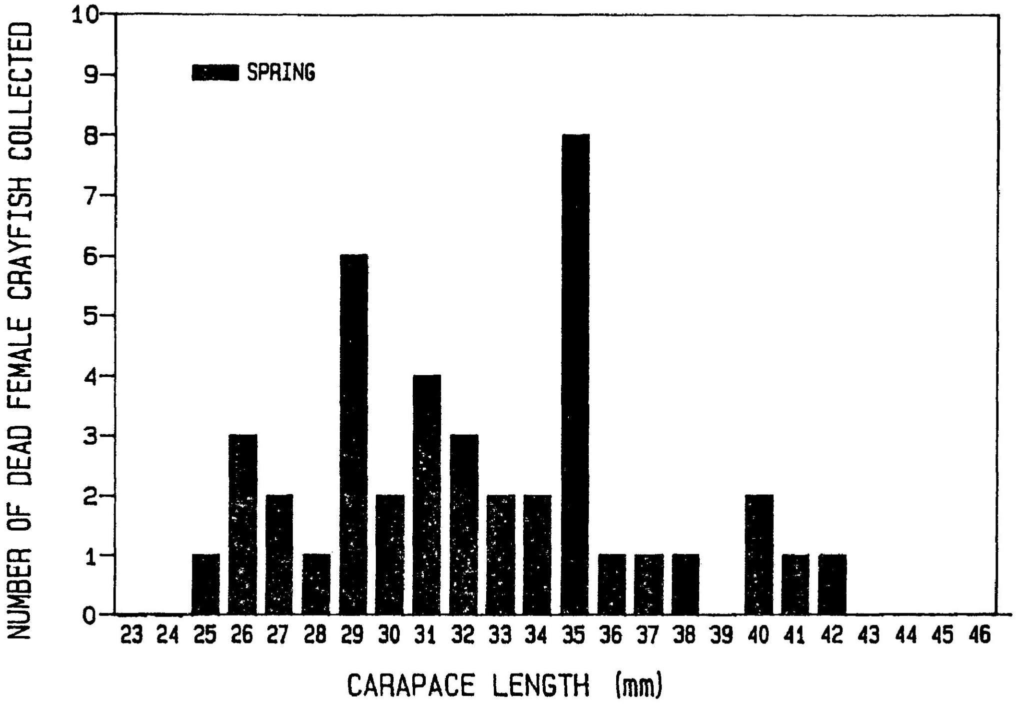
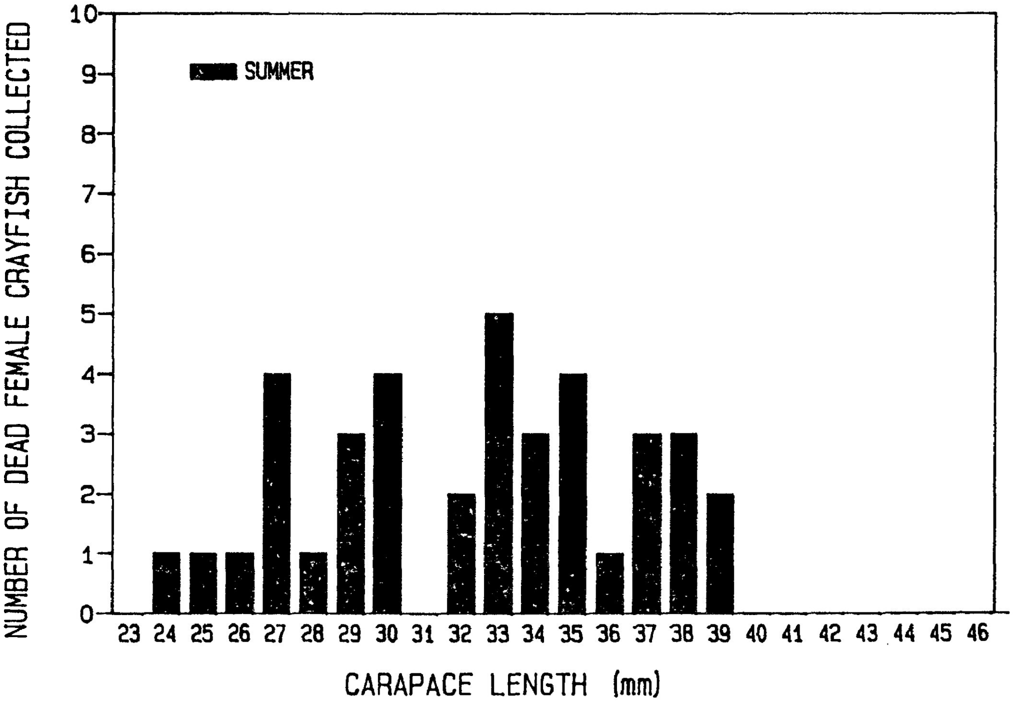


Figure 4. Size frequency of Shallow Lake dead female crayfish collected during the spring and summer sampling periods 1985.

SHALLOW LAKE FEMALE CRAYFISH





Mortality of Dock Lake females was significantly higher in the spring ($P<0.05$) when compared to summer and harvest periods (Tables 1, 2 and 3). Dock Lake male and Shallow Lake female mortality was similar between summer-to-harvest and spring-to-summer periods, respectively (Tables 1, 2 and 3).

In Dock Lake mortality was equal (i.e., non-selective) among size groups as noted by the diffuse size frequency distribution (Fig. 1 and 2). Summer Shallow Lake male mortality was constant over the size range examined (Fig. 3). Female mortality in Shallow Lake was multi-modal, consistent with the size-frequency structure of the population (Fig. 4).

Seasonal Mortality Factors

Dead crayfish were collected during three sampling periods as follows:

Spring Collection

During spring (i.e., from egg extrusion until female moult), June 26 to July 10, 69 dead crayfish were collected (Table 1). Shallow Lake accounted for two-thirds of the crayfish examined (46 of 69), and most of these were females (41 of 46). Although very few Shallow Lake females moulted, three-quarters had damaged appendages (Table 1). Thirty percent of Dock Lake females had moulted and one-half had damaged appendages. Prevalence of porcelain disease was similar between females in both lakes.

Shallow Lake males had a higher prevalence of both porcelain disease and damaged appendages, but fewer had moulted compared to Dock Lake males. There were no size differences between Dock and Shallow Lake males or females. Spring mortality principally effected age I and age II crayfish. Dock Lake mortality appeared moult related. Male and female crayfish in Shallow Lake had a larger proportion of damaged appendages. Shallow Lake males also had a higher prevalence of porcelain disease.

Summer Collection

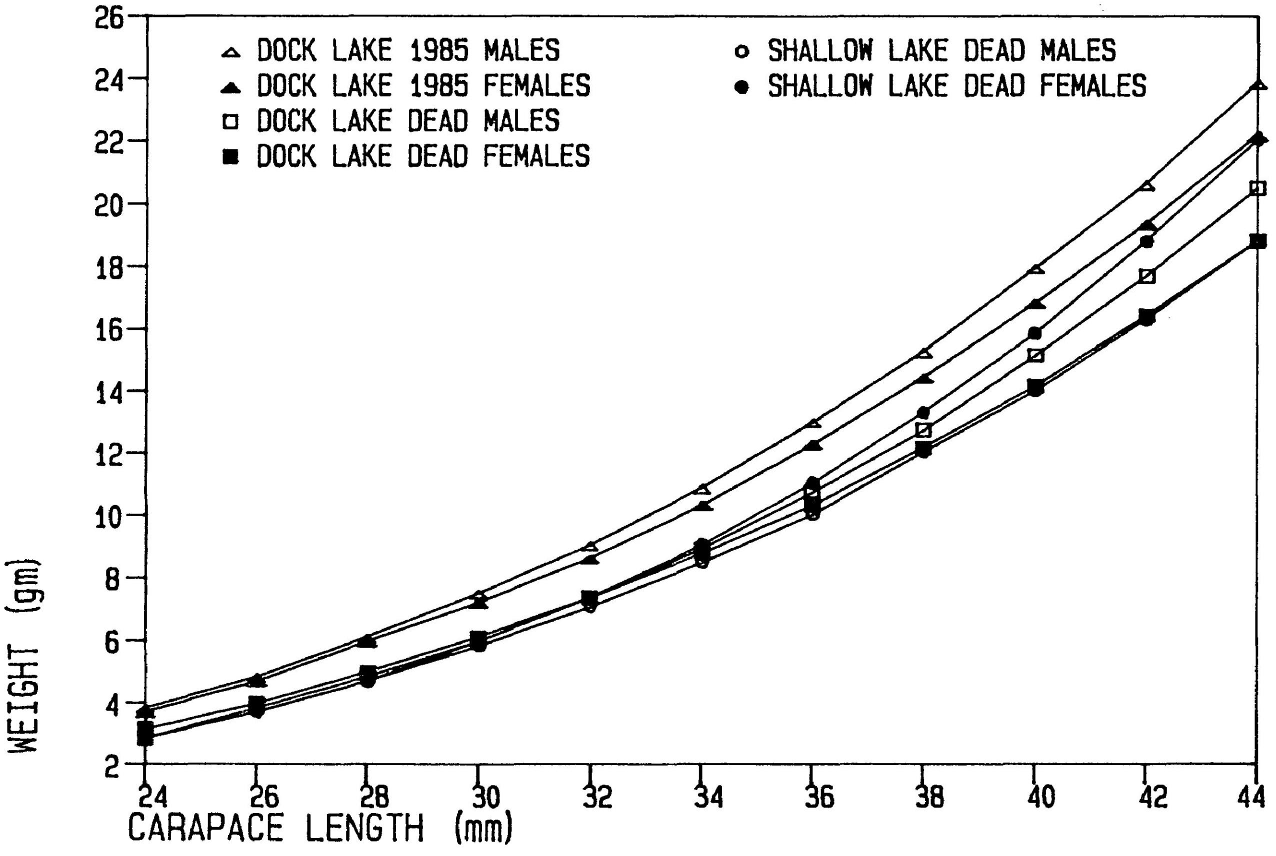
Dead crayfish were collected during summer (July 16 to August 6) i.e., after the male's completed their maturity moult to form I. Almost eighty percent (79 of 99) of the dead crayfish sampled were from Shallow Lake, with approximately equal numbers of males and females (41 males and 38 females) (Table 2). Although the occurrence of damaged appendages was similar between the sexes in Shallow Lake females had a higher prevalence of porcelain disease. In contrast none of the crayfish examined in Dock Lake had porcelain disease. Though Dock Lake females had the same proportion of damaged appendages as Shallow Lake crayfish, only half as many Dock Lake males were similarly affected. Most of the crayfish in both lakes had moulted (94 of 99). During the summer, mortality predominantly affected age I and age II crayfish. While Dock and Shallow Lake females were similar in size, Shallow Lake males were larger ($P<0.03$) than those in Dock Lake. Summer mortality is evidently moult related in both lakes. However in Shallow Lake mortality among crayfish with porcelain disease increases during summer.

Harvest Collection

Harvest of Dock Lake crayfish began on August 7 and lasted until September 2. Shallow Lake was not sampled during this period. All dead crayfish examined had moulted and almost half had damaged appendages (Table 3). Only a small proportion of the males had porcelain disease (1 of 11). Age I males and age II females experienced the highest mortality during the harvest.

In summary the 1985 necropsy samples revealed that Dock Lake crayfish moulted earlier in the spring while during the summer a similar proportion moulted in both lakes. Dead males in both lakes displayed an increased percentage of damaged appendages during the growing season with Shallow Lake males exhibiting the greatest prevalence. While the proportion of Shallow Lake females with damaged appendages decreased during the season damage to females in Dock Lake remained at 45-55% between spring and harvest. Dead females in both lakes had more damaged appendages than males. The prevalence of porcelain disease decreased from spring to summer for males in both lakes and females in Dock Lake. In Shallow Lake, females showed increased prevalence of the disease as the season progressed. Overall Shallow Lake crayfish had higher prevalences of porcelain disease. In contrast only one crayfish sampled during the summer and harvest periods in Dock Lake had porcelain disease.

Figure 5. Relationships between carapace length (mm) and wet weight of Dock Lake 1985 harvest and Dock and Shallow Lake 1985 necropsy sample. Dock Lake linear regression lines, 1985 male harvest: $\log Y=3.031227\log X-3.603801$, $R2=0.99$ ($P<0.00001$); 1985 female harvest: $\log Y=2.949760\log X-3.501430$, $R2=0.99$ ($P<0.00001$); male necropsy sample: $\log Y=3.22596\log X-3.99005$, $R2=0.96$ ($P<0.00001$); female necropsy sample: $\log Y=2.93898\log X-3.55706$, $R2=0.92$ ($P<0.00001$); Shallow Lake regression lines, male necropsy sample: $\log Y=3.06575\log X-3.76492$, $R2=0.92$ ($P<0.00001$); female necropsy sample: $\log Y=-3.41338\log X-4.26737$, $R2=0.98$ ($P<0.00001$), for relationship between logarithmically transformed (Base 10) wet weight (Y) and logarithmically transformed carapace length (X).



△ DOCK LAKE 1985 MALES
▲ DOCK LAKE 1985 FEMALES
□ DOCK LAKE DEAD MALES
■ DOCK LAKE DEAD FEMALES
○ SHALLOW LAKE DEAD MALES
● SHALLOW LAKE DEAD FEMALES
WEIGHT (gm)
CARAPACE LENGTH (mm)
26
24
22
20
18
16
14
12
10
8
6
4
2
24
26
28
30
32
34
36
38
40
42
44

Table 4. Prevalence of **Psorospermium haeckeli** in Dock and Shallow Lake 1985.

TABLE 4. Prevalence of *Psorospermium haeckeli* in Dock Lake and Shallow Lake 1985.

	Number of Crayfish Infected with *Psorospermium haeckeli*															
	Spring				Summer				Harvest				Total			
Sex	Dead		Alive		Dead		Alive		Dead		Alive		Dead		Alive	
	SL[2]	DL[1]	SL	DL	SL	DL	SL	DL	SL	DL	SL	DL	SL	DL	SL	DL
Male	5	10			44	9				11	-	229	46	30		229
Female	41	13	119	120	38	11				13	-	195	79	37	119	315
Total	46	23	119	120	79	20				24		424	125	67	119	544

[1] Dock Lake

[2] Shallow Lake

Physiological Condition Related to Mortality

The intercepts of the length-wet weight power relationships were significantly different ($P<0.01$) between live Dock Lake crayfish and dead crayfish collected in Dock and Shallow Lake in 1985 (Fig. 5). Dock Lake dead crayfish weighed less than similar sized live crayfish. Female dead crayfish in Shallow Lake were heavier than dead males. Mortality was related to weight loss (i.e., poor physiological condition) in both lakes, however Shallow Lake females were heavier than expected because live males are heavier than females at corresponding sizes due to sexually dimorphic growth (Fig. 5). This implies that the physiological condition of Shallow Lake females was not exclusively responsible for mortality.

Crayfish Anomalies and Internal Parasites

During the 1985 harvest of Dock Lake, a total of 5558 crayfish were examined for morphological deformities and anomalies (3284 males and 2274 females). One gynandromorph (0.02% of the sample) was found. It was 36.1 mm in size, weighing 10.447 gm. The oviducts were present at the bases of the third pereiopods. The seminal receptacle (**annulis ventralis**) was between the fourth and fifth pereiopods. The copulatory stylets were form II but reduced in size. Internal examination revealed a functioning ovary containing 209 mature oocytes, however, the seminal receptacle did not have a sperm plug.

All crayfish collected, dead or alive, from both lakes were infected by the parasite **Psorospermium haeckeli** (Table 4). A random sub-sample of 30 individual specimens of this parasite was

Table 5. Abrahamsson's damage index from random sample of intermoult crayfish in Dock and Shallow Lake July 16, 1985.

TABLE 5. Abrahamsson's damage index from random sample of intermoult crayfish in Dock and Shallow Lake, July 16, 1985.

Lake	Sex	Damaged Legs	Carapace Length (mm)	Sample Size (n)
Shallow	M	Yes	37.9(0.67)	24
		No	35.1(0.31)	222
	F	Yes	33.3(1.00)	12
		No	31.9(0.31)	159
Dock	M	Yes	35.8(1.31)[1]	11
		No	32.8(0.42)	130
	F	Yes	33.6(0.94)	14
		No	30.6(0.32)	116

[1] Mean (standard error)

measured. The average size was 135×10^{-3} mm (standard deviation = 9.3; range $110\text{-}155\times10^{-3}$) by 49×10^{-3} mm (standard deviation = 3.1; range $40\text{-}55\times10^{-3}$). All age classes and both sexes were infected. Intensity of infection was highest in the musculature and digestive tract. Lower intensities being prevalent in the reproductive system and heart.

Abrahamsson's Index of Damaged Appendages

Damaged intermoult crayfish, regardless of sex or lake, were equally prevalent in the random sample (July 16) (Table 5). Different sizes were effected with damaged males in both lakes being larger than intact individuals ($P<0.005$). However while Dock Lake damaged females were larger than undamaged females ($P<0.005$) Shallow Lake females, whether impaired or not, were similar in size.

Male crayfish, classified as deformed or intact, were larger than similarly classified females in Shallow Lake ($P<0.002$). In contrast only uninjured males were larger than females in Dock Lake ($P<0.001$). This indicates that intraspecific aggression presumably affects all Shallow Lake females regardless of size. In contrast only larger females in Dock Lake are similarly affected.

Table 6. Age- and sex-specific instantaneous total mortality rates (Z) for Dock and Shallow Lake male and female crayfish 1976-1985.

TABLE 6. Age- and sex-specific instantaneous total mortality rates (Z) for Dock and Shallow Lake male and female crayfish 1976-1985.

Lake	Age Interval	Sex	Time Interval									
			1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Shallow	Egg-YOY	M	1.95	2.21	3.61	4.22	4.30	3.66	4.60	5.10	4.51	5.58
		F	2.31	2.13	3.64	4.37	3.97	4.32	4.73	5.09	3.89	5.26
Dock	Egg-YOY	M	2.78	2.42	3.76	3.36	3.07	3.24	3.34	3.53	3.74	4.21
		F	2.96	2.80	3.52	2.92	3.21	3.24	3.02	3.59	3.54	4.60
			1976-1977	1977-1978	1978-1979	1979-1980	1980-1981	1981-1982	1982-1983	1983-1984	1984-1985	
Shallow	YOY-I	M	2.07	1.59	1.37	0.41	0.63	1.08	0.68	0	0.41	
		F	2.31	1.55	1.65	0.12	0.33	0.23	0.12	0	0	
Dock	YOY-I	M	1.77	1.21	1.32	1.38	1.48	0.69	0.28	0.39	0.26	
		F	1.60	0.66	1.48	0.89	0.92	0.81	0.47	0.52	0.44	
Shallow	I-II	M	1.36	0.85	0.77	0.55	0.32	0.21	0.07	0.23	0	
		F	0.37	0.37	0.97	0.86	0.99	0.12	0.08	0.27	0	
Dock	I-II	M	0.46	0.19	0.99	1.02	0.69	0.53	1.20	1.24	0.99	
		F	0.74	0.27	1.04	1.26	0.49	0.25	0.68	0.75	0.44	
Shallow	II-III	M	1.78	2.01	2.70	4.23	3.02	3.06	0.56	3.18	2.04	
		F	2.93	1.78	1.78	2.83	3.03	1.77	0.34	1.74	2.72	
Dock	II-III	M	2.30	3.87	3.85	2.65	2.32	2.49	1.44	2.18	2.90	
		F	3.04	1.94	2.92	4.08	2.25	2.67	2.88	1.61	3.61	
Shallow	III+	M	3.22	3.64	3.66	3.30	2.08	3.53	3.83	5.91	3.50	
		F	2.77	3.64	4.23	4.09	3.40	2.89	4.58	6.85	5.12	
Dock	III+	M	2.08	3.30	2.08	2.83	3.50	3.50	3.66	4.48	4.03	
		F	3.37	2.64	3.76	3.66	2.20	3.40	3.69	4.32	4.99	

Temporal Variation in Mortality Patterns

There was an adjustment in age- and sex-specific mortality rates following the increase of nominal fishing pressure from 150 trap-days in 1977 to 1350 trap-days in 1978. A response to exploitation is exemplified by the changing pattern of mortality rates in Dock Lake between the hatching (egg/age 0-to-young-of-year (YOY)), juvenile (YOY-to-age I), and adult (age I-to-age II) life stages (Table 6).

Hatching mortality rates were similar between the sexes in each lake. However Shallow Lake male and female mortality rates during this life stage were higher ($P<0.03$) than in Dock Lake.

Juvenile mortality rates were similar between males and females in Shallow Lake, and Dock Lake males. However Dock Lake female juvenile mortality differed. Their rate was higher than that of Shallow Lake females ($P<0.03$) or Dock Lake males (excluding 1980-81). This is the exact life stage at which females mature (YOY-to-age I).

Shallow Lake male and female adult mortality rates were similar. Following recruitment to the exploitable stock at age I Dock Lake male mortality markedly increased as expected. Dock Lake male adult mortality rate was higher than Dock Lake females (excluding 1978-79 and 1979-80) or Shallow Lake males and females ($P<0.02$). From 1980 until 1984, harvesting accounted for all adult male mortality. Males also mature during this life stage (age I-to-age II).

There is no difference in male or female age II-to-age III mortality rates between the two populations. Consequently the low hatching mortality rate resulted in higher YOY production in Dock

Figure 6. Time trend in male conditional mortality rates for Dock and Shallow Lake 1976 to 1985.

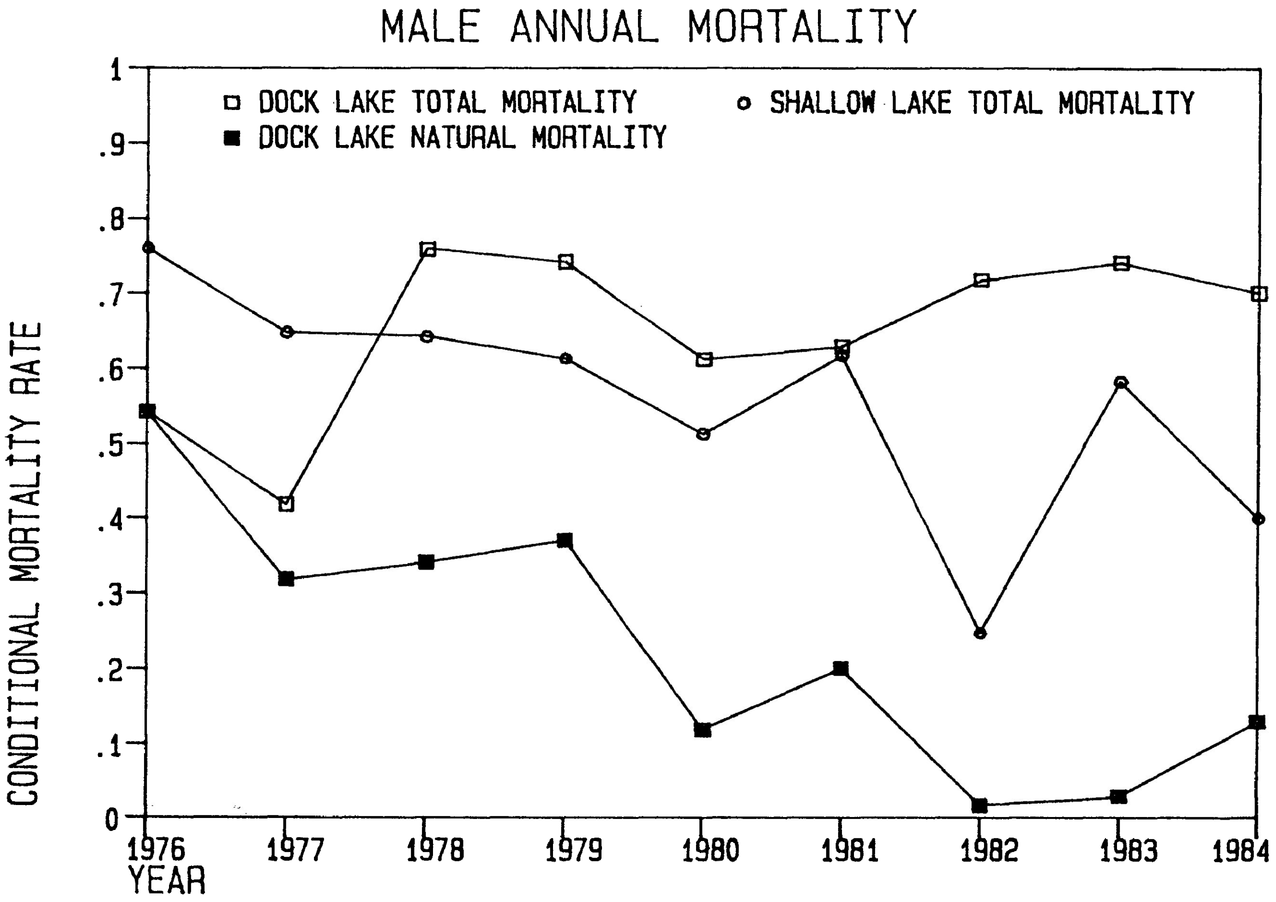
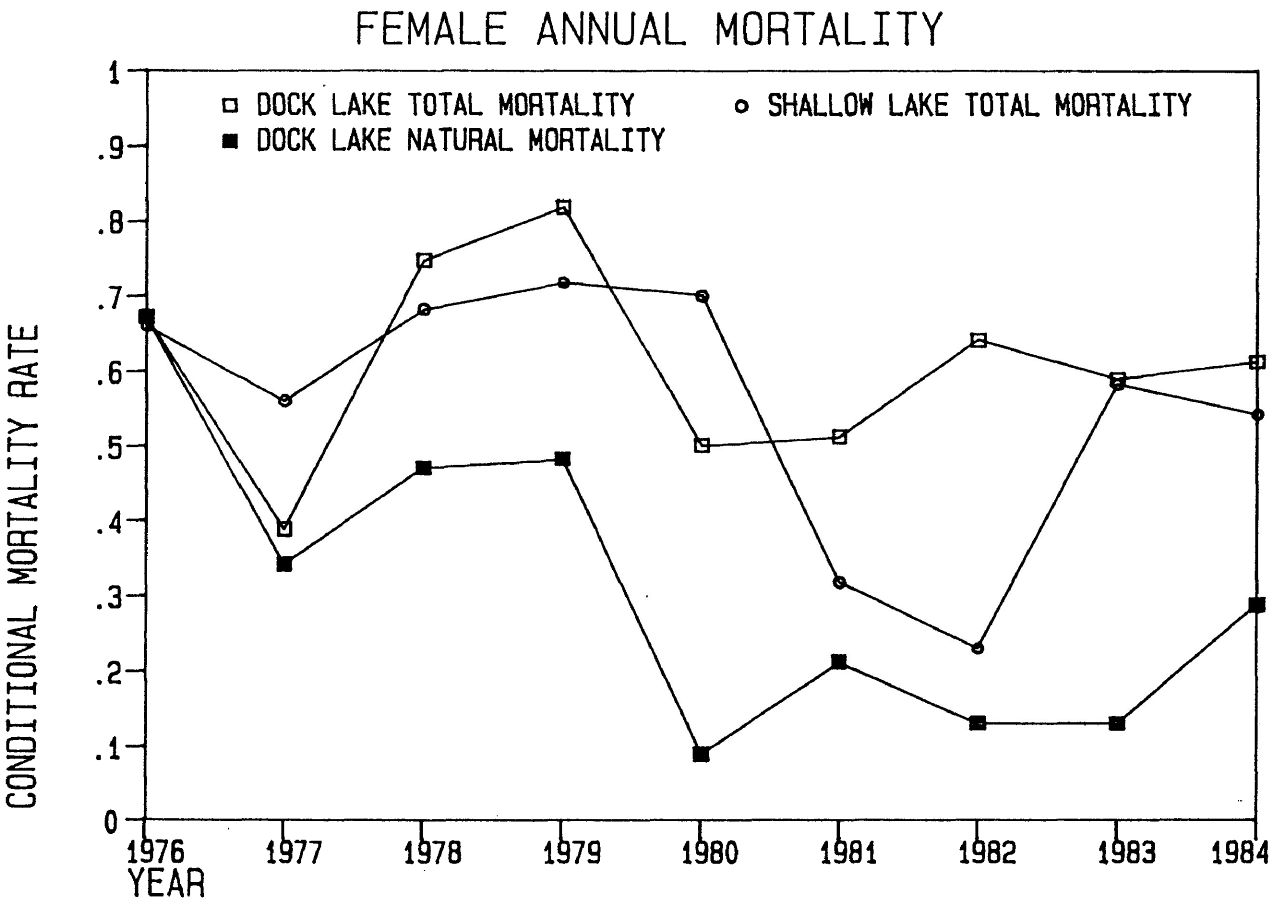

MALE ANNUAL MORTALITY
□ DOCK LAKE TOTAL MORTALITY
○ SHALLOW LAKE TOTAL MORTALITY
■ DOCK LAKE NATURAL MORTALITY
CONDITIONAL MORTALITY RATE
1
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
1976
1977
1978
1979
1980
1981
1982
1983
1984
YEAR

Figure 7. Time trend in female conditional mortality rates for Dock and Shallow Lake 1976 to 1985.


FEMALE ANNUAL MORTALITY
□ DOCK LAKE TOTAL MORTALITY
○ SHALLOW LAKE TOTAL MORTALITY
■ DOCK LAKE NATURAL MORTALITY
CONDITIONAL MORTALITY RATE
1
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
1976
1977
1978
1979
1980
1981
1982
1983
1984
YEAR

Lake. However at sexual maturity Dock Lake's sex-specific mortality rates increased (Table 6). Dock Lake females experience higher mortality before recruitment to the exploitable stock (i.e., YOY-to-age I). In contrast Dock Lake males sustain increased mortality upon recruitment (i.e., age I-to-age II).

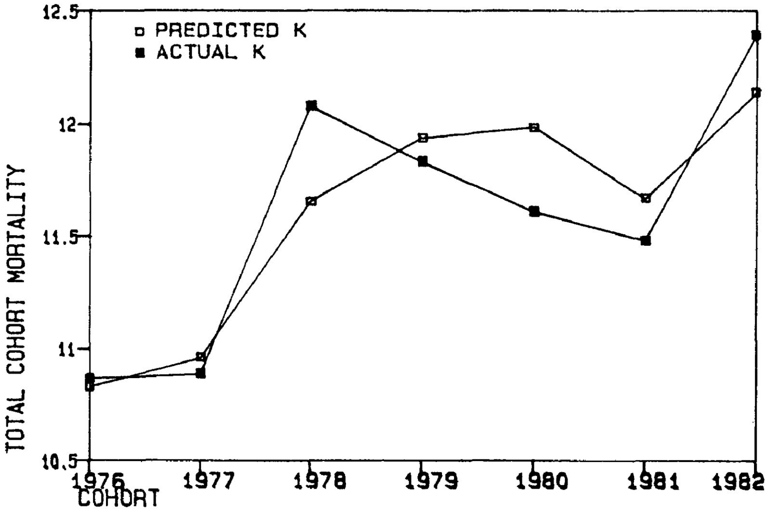
The compensatory response of the exploited stock (age I to age III) is best seen in the time trend in conditional mortality rates. Male natural mortality decreases in both lakes (Fig. 6) but more so in Dock Lake than in Shallow Lake (natural mortality = total annual mortality). Total annual mortality remains relatively constant since the 1978 harvest in Dock Lake. Increased recruitment, a result of increased YOY production, compensates for the sustained higher total annual mortality of Dock Lake males. Since 1980 Dock Lake fishing mortality has increased at the same rate as natural mortality has decreased.

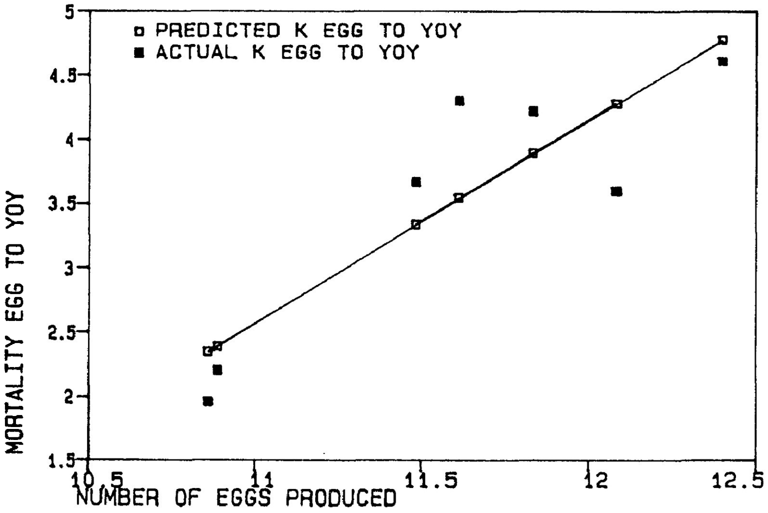
Dock Lake female natural mortality decreases in a step-wise manner from the beginning of exploitation up until 1980, and then again from 1980 until 1985 (Fig. 7). In Shallow Lake female natural mortality (= total annual mortality) remains relatively constant, except for 1981-82 and 1982-83. Dock Lake female total annual mortality has remained relatievly constant since the harvest of 1980.

The compensatory response in natural mortality, coupled with increased recruitment, has stablized both total annual mortality and resilience to increased levels of exploitation. Effort increased from 150 trap-days (30 traps for 5 days) in 1977 to 1350 trap-days (150 traps for 9 days) in 1978 and then to 2600 trap-days (200 traps for 13 days) in 1979. This resulted in an

Figure 8. Key factor analysis of Shallow Lake male 1976 to 1982 cohorts. Regression lines, $Y=0.4884621X+9.881619$, $R2=0.77$ ($P<0.01$), for relationship between total cohort mortality (Y) and egg-to-YOY mortality (X); $Y=1.579697X-14.80920$, $R2=0.77$ ($P<0.01$), for relationship between egg-to-YOY mortality (Y) and egg density (X); $Y=0.9338172X-6.433186$, $R2=0.88$ ($P<0.005$), for relationship between YOY-to-age I mortality (Y) and YOY density (X).

KEY-FACTOR ANALYSIS: SHALLOW LAKE MALES





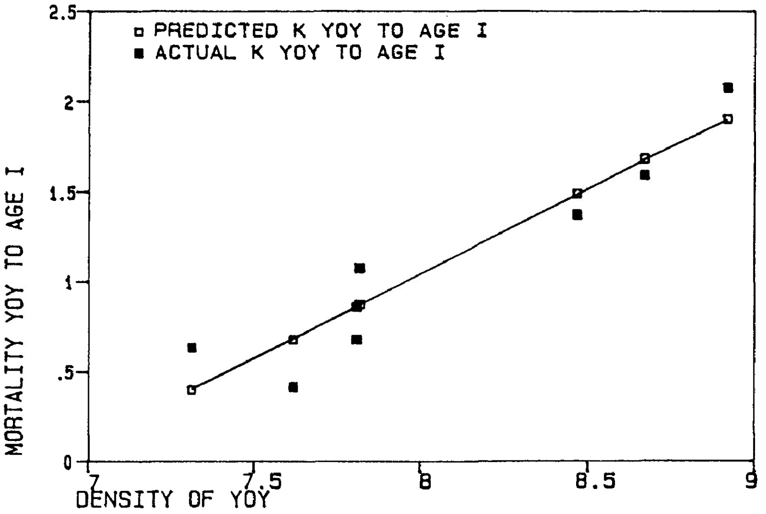
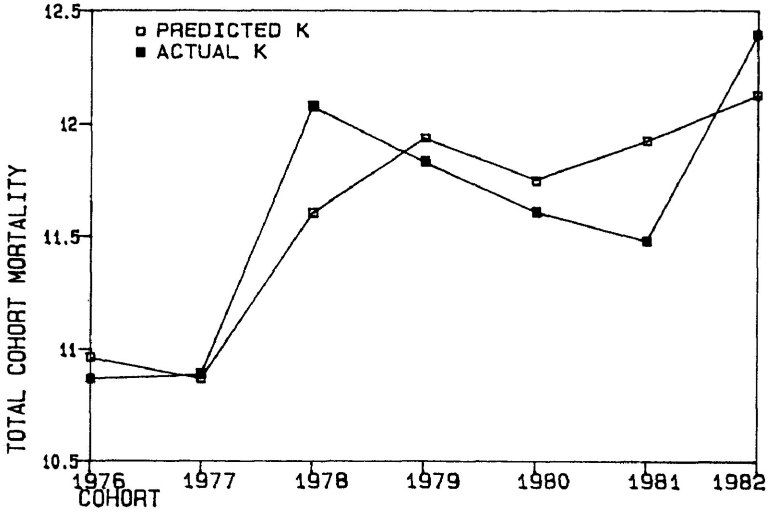
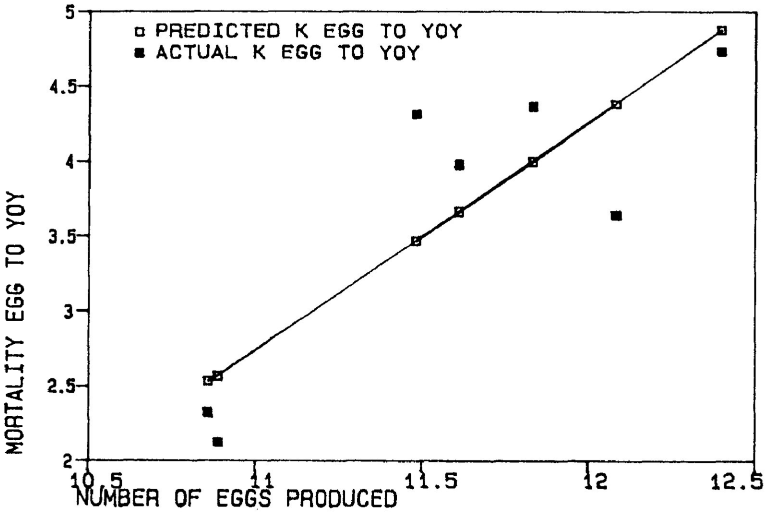


Figure 9. Key factor analysis of Shallow Lake female 1976 to 1982 cohorts. Regression lines, $Y=0.4770784X+9.858069$, $R2=0.72$ ($P<0.025$), for relationship between total cohort mortality (Y) and egg-to-YOY mortality (X); $Y=1.519927X-13.98315$, $R2=0.72$ ($P<0.0.025$), for relationship between egg-to-YOY mortality (Y) and egg density (X); $Y=1.3347X-9.716067$, $R2=0.82$ ($P<0.0.01$), for relationship between YOY-to-age I mortality (Y) and YOY density.

KEY-FACTOR ANALYSIS: SHALLOW LAKE FEMALES





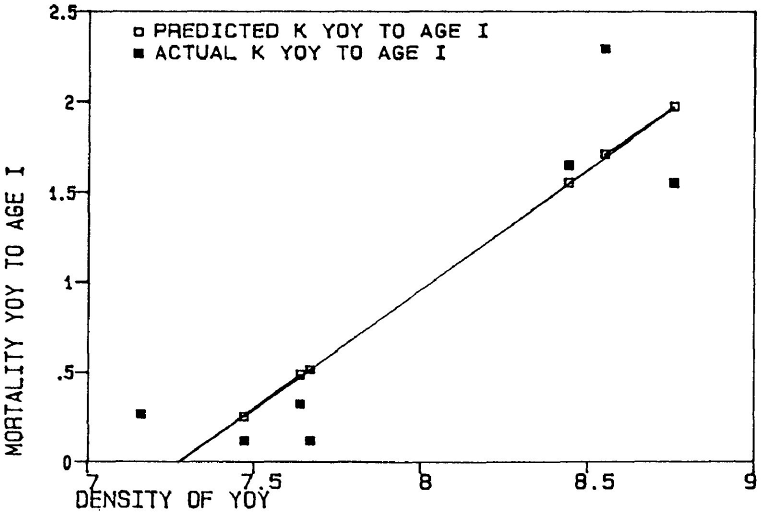
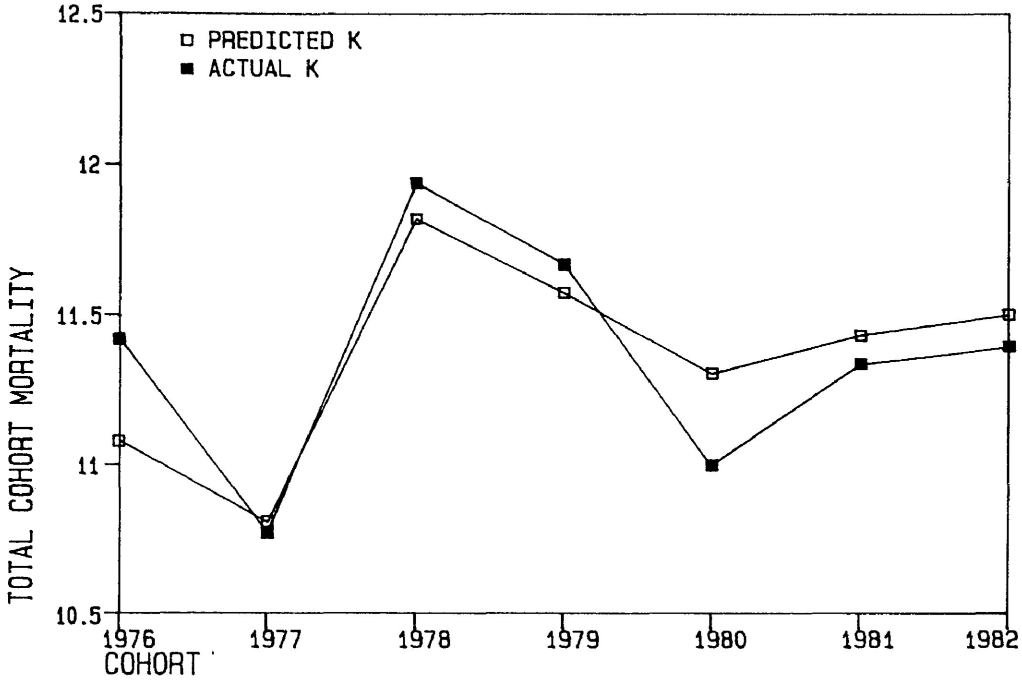
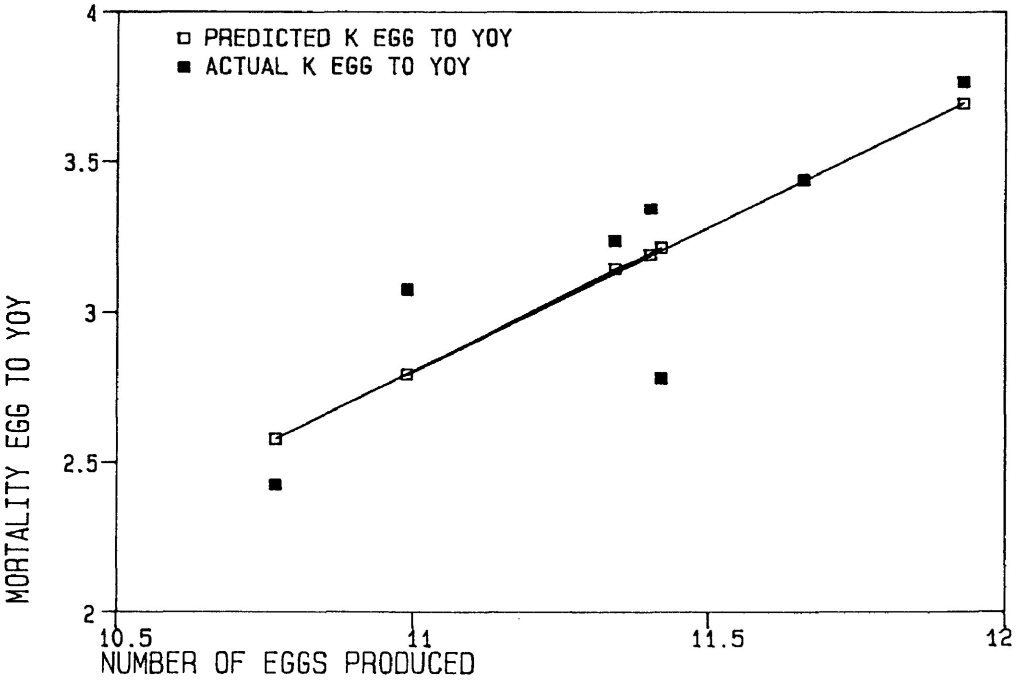
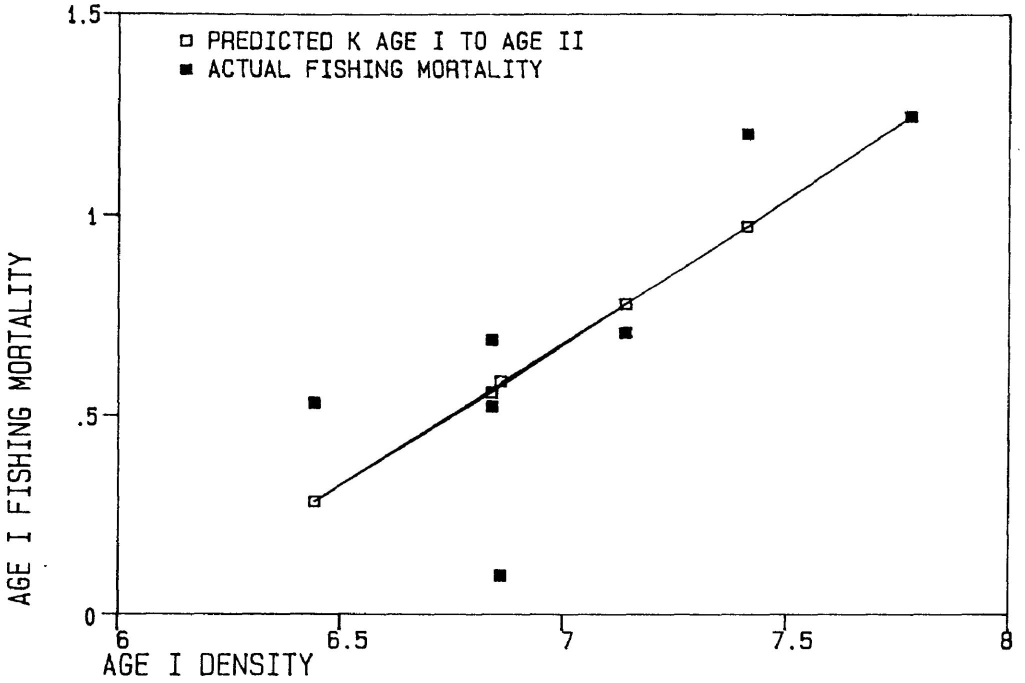


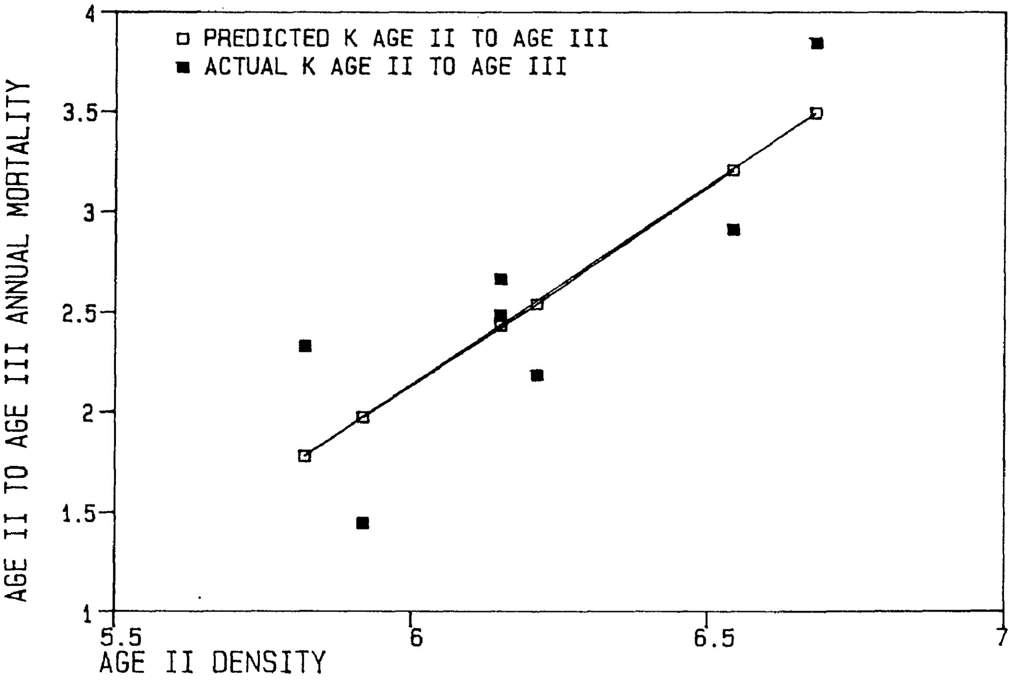
Figure 10. Key factor analysis of Dock Lake male 1976 to 1982 cohorts. Regression lines, $Y=0.7477243X+9.002591$, $R2=0.73$ ($P<0.025$), for relationship between total cohort mortality (Y) and egg-to-YOY mortality (X); $Y=0.9724934X-7.895393$, $R2=0.73$ ($P<0.025$), for relationship betwen egg-to-YOY mortality (Y) and egg density (X); $Y=0.7186822X-4.350718$, $R2=0.62$ ($P<0.05$), for relationship between age I-to-age II fishing mortality (Y) and age I density (X); $Y=1.976086X-9.721502$, $R2=0.70$ ($P<0.0.25$), for relationship between age II-to-age III total mortality (Y) and age II density (X).

KEY-FACTOR ANALYSIS: DOCK LAKE MALES






□ PREDICTED K AGE I TO AGE II
■ ACTUAL FISHING MORTALITY
AGE I FISHING MORTALITY
0
.5
1
1.5
6
6.5
7
7.5
8
AGE I DENSITY


□ PREDICTED K AGE II TO AGE III
■ ACTUAL K AGE II TO AGE III
AGE II TO AGE III ANNUAL MORTALITY
1
1.5
2
2.5
3
3.5
4
5.5
6
6.5
7
AGE II DENSITY

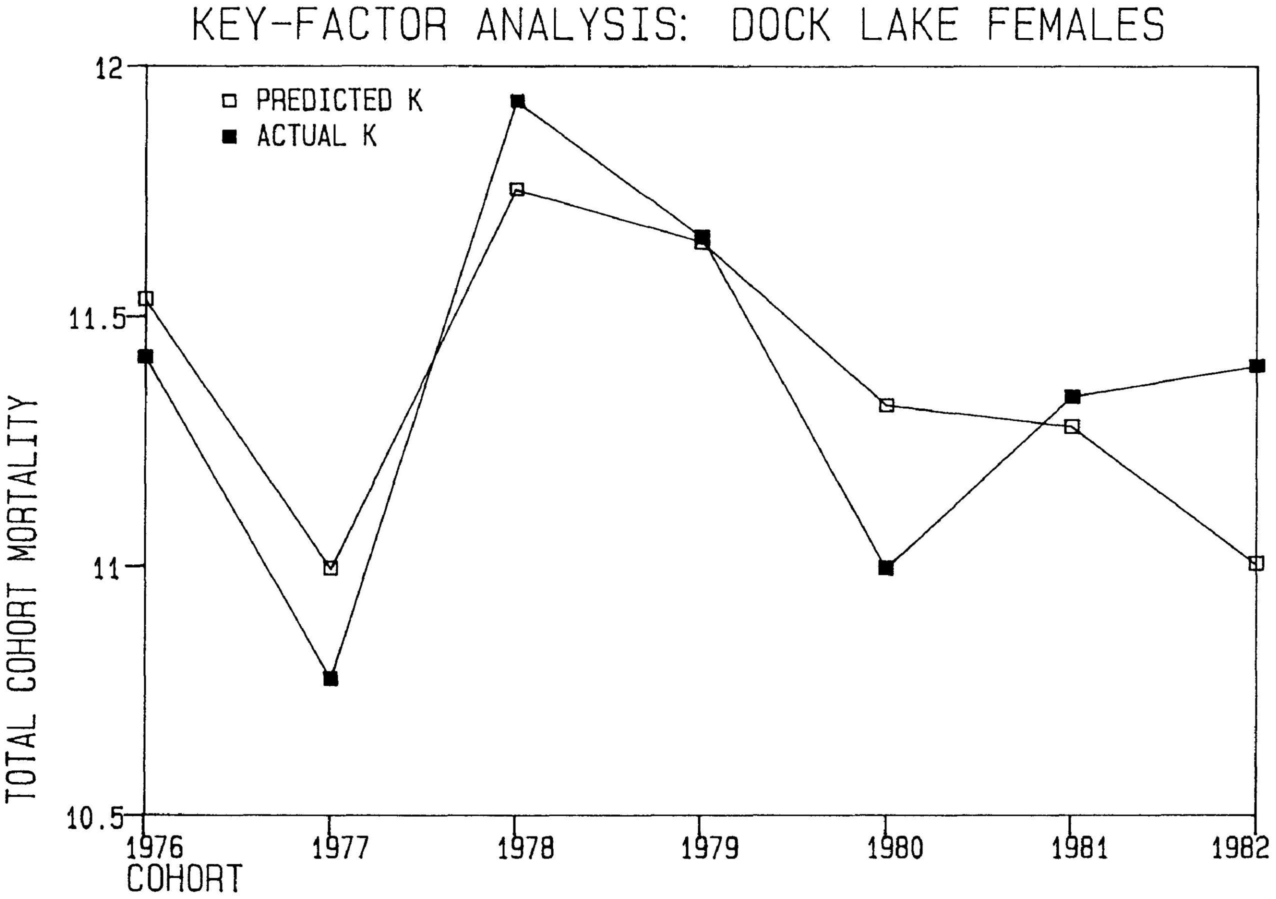
initial increase in total annual mortality from additive fishing mortality. However natural mortality remained unchanged during this period and the population in Dock Lake declined from 4334 in 1978, to 3005 in 1979 and finally 2543 in 1980. The population response lagged 2 years behind the increase in effort (both nominal effort and fishing power). The population remained unchanged in size in 1981 (2692 crayfish) but increased dramatically to 4300 crayfish in 1982 with the compensatory decrease in natural mortality. This population has continued to increase until 1985 (9273 crayfish) even though effort had increased to 4000 trap-days (200 traps for 20 days).

Key-Factor Analysis

Major fluctuations in the 1976-82 Shallow Lake male and female cohorts were caused by mortality within the hatching stage (i.e., the `key factor') (Fig. 8 and 9). Shallow Lake male and female mortality at both the hatching and juvenile stage are strongly density-dependent. Subsequent life stages exhibit variable density independent mortality.

Dock Lake 1976-82 male cohorts also exhibit strong regulation during the hatching stage (Fig. 10) with mortality strongly density-dependent. However juvenile mortality becomes both density independent and quite variable. Adult fishing mortality is strongly compensatory while in contrast natural mortality is not. At the age II-to-age III stage total mortality is also strongly density-dependent because fishing and natural mortality are compensatory.

Figure 11. Key factor analysis of Dock Lake female 1976 to 1982 cohorts. Regression lines, $Y=0.4910573X+9.5288592$, $R2=0.60$ ($P<0.05$), for relationship between total cohort mortality (Y) and combined egg-to-age I mortality (X). Egg-to-YOY mortality is relatively constant 3.0947 (standard error=0.0932) and YOY-to-age I mortality is weakly density-dependent, $Y=1.103421X-7.998161$, $R2=0.46$ ($P<0.10$), where Y is YOY-to-age I mortality and X is YOY density.


KEY-FACTOR ANALYSIS: DOCK LAKE FEMALES
□ PREDICTED K
■ ACTUAL K
TOTAL COHORT MORTALITY
12
11.5
11
10.5
1976
1977
1978
1979
1980
1981
1982
COHORT

The key factor determining Dock Lake female cohort densities is mortality from the egg-to-age I stage (Fig. 11). Relatively constant hatching mortality interacts with weakly density-dependent juvenile mortality to produce a compensatory relationship. Beyond age I mortality rates are highly variable and density independent.

DISCUSSION

Exploitation decreased seasonal mortality of Dock Lake crayfish. Female mortality in Dock Lake is highest in spring. During spring, moult related mortality predominates in Dock Lake, while in Shallow Lake, female mortality is more related to intraspecific aggression (inferred from the higher prevalence of damaged appendages). Spring female mortality is higher in Shallow Lake. Little male mortality occurs during the spring in either lake.

In summer, mortality in both lakes becomes moult related, however Shallow Lake crayfish suffer a higher prevalence of porcelain disease. While there are no differences between male and female summer mortality rates within lakes, Shallow Lake crayfish have higher mortality rates than Dock Lake.

While the proportion of dead males with damaged appendages increases from spring to harvest in Dock lake and from spring to summer in Shallow Lake, the incidence of damaged appendages is higher in Shallow Lake. The percentage of dead females in Dock Lake with damaged appendages remains consistently at 45-55% while in Shallow Lake the proportion of females with damaged appendages decreases during the growing season.

The prevalence of porcelain disease decreases from spring to summer for Dock Lake males and females, and Shallow Lake males but in Shallow Lake females it increases. Overall porcelain disease is more common in the control lake population though the number infected by this parasite is undoubtedly underestimated by the sampling method employed (O'Keeffe and Reynolds 1981).

The presence of **Psorospermium haeckeli** in these populations is the first known record from North America and in the genus **Orconectes**. Nylund and Westman (1978) described the European records of this parasite: in **Astacus astacus** L. and **Astacus leptodactylus** Esch in Germany, in **A. astacus** and **Cambarus affinis** Say in Poland, in **A. astacus** and **Pacifastacus leniusculus** Dana in Sweden and **A. astacus** in Finland. This parasite is apparently well adapted to these hosts (Unestam 1974). All crayfish examined during the summer of 1985, regardless of age, sex, season, or condition were infected. This parasite is not considered to be a mortality factor in these populations.

The random size distribution of dead male and female crayfish in Dock Lake indicates non-selective mortality (Fig. 1 and 2). The constant number of dead male crayfish per size class in Shallow Lake signifies that mortality is independent of abundance (Fig. 3). In contrast female mortality in Shallow Lake is proportional to abundance (Fig. 4). Exploitation produces significant changes in seasonal mortality. Dock Lake crayfish have lower spring and summer mortality than Shallow Lake's. Mortality in Dock Lake is generally moult related. In contrast

Shallow Lake male mortality results from porcelain disease and seasonally increasing intraspecific aggression. Spring female mortality is related to intraspecific aggression in Shallow Lake. While in summer, Shallow Lake female mortality is associated with both intraspecific aggression and porcelain disease. Dead Dock Lake crayfish and Shallow Lake males were in poor physiological condition. Shallow Lake females were in relatively better condition and cause of death was apparently not related to weight loss (Fig. 5).

Dock and Shallow Lake intermoult samples had the same relative number of individuals with damaged appendages (e.g. 7-11%). However, Dock Lake total density was greater than Shallow Lake's in 1985 (Shallow Lake = $1.03.m^{2.-1}$; Dock Lake = $1.47.m^{2.-1}$). Female densities were similar (Shallow Lake =$0.68.m^{2.-1}$; Dock Lake = $0.77.m^{2.-1}$) but male densities differed by a factor of two (Shallow Lake = $0.35.m^{2.-1}$; Dock Lake = $0.70.m^{2.-1}$). Therefore intraspecific aggression affected Shallow Lake crayfish more than Dock Lake crayfish (i.e., same proportions with damaged appendages although absolute densities and relative densities between sexes differed). Damaged males were larger than undamaged males in both lakes. Though Dock Lake damaged females were larger than undamaged females, Shallow Lake damaged and undamaged females were similar in size. The percentage of crayfish with damaged appendages does not serve as an surrogate variable of population density or stress as proposed by Abrahamsson (1966). A more useful indicator would be to calculate the mean size difference between damaged and undamaged individuals (especially females) in a random sample.

In exploited Dock Lake age- and sex-specific mortality rates regulate population densities. The initial increase in effort and fishing power in 1978 actually enhanced hatching survival. The density-dependent survival in the early stages of the life cycle determined population density in both Dock and Shallow Lakes. However Shallow Lake crayfish experienced higher mortality from hatching and density-dependent mortality during the juvenile life stage. These mortalities limited population growth in Shallow Lake.

Mortality of sexually mature adults in both lakes is density independent and variable. Increased stress on adult males (life stage when sexual maturity is obtained) has an important effect on crayfish population regulation. When Momot and Gowing (1977a, b and c) exploited O. **virilis** in two marl lakes in Michigan they harvested crayfish using a size limit of 30 mm. Males attained sexual maturity by age I at a mean size of 30-31 mm (Momot 1967) and so the size limit protected the maturing male crayfish. Declining recruitment resulted from losses of nursery microhabitat between pre-exploitation and exploitation periods (Momot and Gowing 1977c). The key factor analysis used in the present study indicates that increased fishing of adult males effectively reduces the impact that density-dependent hatching and juvenile mortality has on population regulation. The decline in available habitat combined with the high densities of age I+ crayfish probably served as a negative biotic feedback in the Michigan populations. In fact the population collapsed in West Lost despite size limits and application of an equilibrium yield harvest based on these limits (Momot and Gowing 1977c). A possible mechanism regulating density could be conspecific aggression between hatchlings and juvenile males. The temporal and spatial distribution of yearling crayfish overlapped with that of fecund females as well as YOY distribution in these lakes (Momot 1967). Therefore the shrinking nursery habitat served to concentrate newly hatched YOY within the area of highest juvenile density exacerbating the regulatory effect.

In contrast the present harvesting scheme in Dock Lake removes age I crayfish in proportion to their abundance. At high levels of effort, all adult mortality is due to exploitation. This apparently reduces the inhibitory effect of these age groups on YOY survival and diminishes density-dependent juvenile mortality. The rate of population growth increases as a result. If such a mechanism is common to other crustaceans, then the use of size limits to protect maturing size groups from exploitation decreases population growth potential.

Total annual mortality increased in Dock Lake as nominal fishing effort increased to 1350 trap-days in 1978. This harvest of 150 traps for 9 days removed 35% of the total exploitable stock, age I+ and older (i.e., harvesting removed 40% of the males and 25% of the females). However, Dock Lake's exploitable stock declined from 4334 crayfish in 1978 to 2543 in 1980 as a result of an excessive total annual mortality time lag (Fig. 6 & 7). High female mortality in these years caused to population to decline. Changes in harvesting intensity selectively removed smaller females that would have otherwise survived to reproduce the following spring (Morgan 1987). This selectivity coupled with spring mortalities (of the larger females) resulted in additive mortality and the population decreased (from recruitment overfishing). Since then the crayfish population of Dock Lake has continued to increase even though annual harvests of 4000 trap-days (200 traps for 20 days) take 60% of the exploitable stock.

As a result of our analysis of crayfish mortality we propose that a threshold mortality index be used as a management measure to maintain or increase population density. Crayfish stocks should be managed so that total annual mortality is less than 75% of the vulnerable stock. Both Dock and Shallow Lake populations exhibit high annual losses of between 60% to 70% of crayfish age I and older. This does not detrimentally effect population growth because adult mortality is balanced by annual recruitment during the juvenile life stage. Consequently, exploitation merely substitutes for the high natural mortality commonly experienced by crayfish populations. Increases in Shallow Lake population density occur only as natural mortality falls. In contrast, in Dock Lake's population growth occurs with a constant but intense total annual mortality rate. Exploitation apparently substitutes for natural mortality up to a stable maximal limit balanced by increasing levels of recruitment. Therefore, in our opinion, at least one-third to one-half of the available population of northern crayfish, or similar crustaceans, can be safely harvested.

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EXPLOITATION

Morgan, G.E. & W.T. Momot. 1987. Analysis of harvest patterns of the crayfish **Orconectes virilis** in northwestern Ontario. In preparation.

ABSTRACT

Harvesting Dock Lake crayfish with modified minnow traps baited with fresh fish, changed the pattern of exploitation as nominal effort increased from 150 trap-days in 1977 to 6000 trap-days in 1985. Changes in age- and sex-specific catchability were determined by interactions of: sampling intensity, duration of harvest and behavioural responses. Gear saturation occurred with the use of 200 minnow traps (i.e., linear trap spacing of 3 m). Increasing the effort from 4000 trap-days to 6000 trap-days (i.e., 200 traps for 20 days vs. 200 traps for 30 days) failed to increase exploitation rates. This is the result of time saturation. At higher levels of nominal effort, large males dominated early catches (e.g., 20-30% of total harvested). However by the end of the harvest their proportion had decreased to less than half (e.g., 10%). These large males prevented smaller crayfish from entering the traps. Exploitation rates determined from mark-recapture techniques and catch-per-unit-effort (CPUE) abundance estimates underestimated actual removal rates.

The functional response between female catchability and population density predisposes the stock to overfishing at low population densities (i.e., depensatory mortality). This invalidates CPUE as a index of female relative abundance. Male CPUE was inversely related to sampling intensity. For assessment purposes, we propose that sampling design should standardize the effort per unit of area (for the area of the littoral zone) as opposed to sampling with constant effort, and use relative male abundance as the basis of a CPUE index (in exploited populations only). Even with a forty-fold increase in nominal effort, we could not harvest more than 60% of the total exploitable stock, age I+ (approximately 75% of the males, 50% of the females). The population is thus protected from biological overfishing regardless of effort. The harvest fluctuates in relation to the available exploitable stock (i.e., a fixed proportion is harvested for each level of nominal effort up to a maximum of 60%). Development of active capture gear would be needed to increase harvests and significantly improve the feasibility of economically exploiting northern crayfish stocks.

INTRODUCTION

The potential for commercially harvesting the crayfish **Orconectes virilis** (Hagen) has been investigated in Vermont (Nolfi and Miltner 1978; Nolfi 1981), Wisconsin (Threinen 1958) and Michigan (Momot and Gowing 1977). Specific management procedures for these wild stocks were considered unnecessary. This is because males are much more vulnerable to passive fishing gear so that in these fisheries males comprised over 95% of the harvest. This inadvertently protects the spawning stock (Threinen 1958; Momot and Gowing 1977).

Momot and Gowing (1977) examined the effect of attempting a maximum sustained yield strategy for crayfish populations inhabiting oligotrophic lakes. Only crayfish >30 mm in carapace length (C.L.) were harvested. This size limit was intended to protect the sexually mature females as well as being considered a possible minimum marketable size for crayfish (Momot pers. comm.). Threinen (1958) and Nolfi (1981) considered 37-38 mm C.L. as the lower size limit acceptable as human food.

An intensive study of crayfish population dynamics in two small marl lakes in northwestern Ontario began in 1976 employing a control-treatment experimental design (Momot 1978). This design monitored responses of the populations related to environmental variation and perturbation. Harvesting began in Dock Lake in 1977 at a nominal effort of 150 trap-days (30 traps for 5 days) and increased forty-fold by 1985 to 6000 trap-days (200 traps for 30 days). During this time fishing effort and fishing intensity changed. All crayfish vulnerable to the gear, excluding incidental catches of young-of-year (YOY), were harvested.

This paper discusses both the data necessary for an analytic assessment as well as management of northern stocks of the crayfish **Orconectes virilis** at these increasing levels of nominal fishing effort. Our long-term study provides a consistent approach to the management of northern crayfish populations and presents guidelines based on the need to protect crayfish stocks from possible over-exploitation.

STUDY AREA AND METHODS

The study area's physical and chemical characteristics as well as general methods have been described elsewhere (Momot 1978; Morgan 1987); only additional methods particular to this study are described here.

Harvesting of the crayfish in Dock Lake began in 1977 at a nominal fishing effort of 150 trap-days (30 traps for 5 days). A trap-day is one modified minnow trap fished 24 hours. Nominal fishing effort (f) refers to the total number of capture units multiplied by the duration of sampling (Ricker 1975). We employed as passive gear modified, wire-mesh, cylindrical, funnel-ended minnow traps (44.5 cm long X 23 cm at largest diameter with both entrance holes expanded to 3-5 cm diameter, mesh of 6.25 mm and weighing approximately 0.7 kg) baited with 40-60 gm of frozen fish (usually American Smelt, **Osmerus mordax** (Mitchill)). Effort increased to 1350 trap-days (150 traps for 9 days) in 1978. From 1979 to 1981 the effort was raised to 2600 trap-days (200 traps for 13 days). Again in 1982 the effort was increased, to 4000 trap-days (200 traps for 20 days). This level of fishing effort was maintained for 1983 and 1984. However in 1984 the fishing intensity changed without changing the fishing effort (250 traps for 16 days). Fishing intensity or sampling intensity is the fishing effort per unit area (Beverton and Holt 1957). Beginning in 1985 the nominal effort was increased once more to 6000 trap-days (200 traps for 30 days). Annual harvesting began after the male maturity moult to form I. Trapping occurred only during intermoult periods and water temperatures always exceeded 13 °C, the point above which catches are insensitive to temperature (Capelli 1975). We thereby hoped to avoid seasonal changes in trapability related to behaviour or abiotic factors.

All harvested crayfish were externally sexed and measured to the nearest 0.5 mm from the tip of the rostrum to the posteriomedial edge of the carapace using vernier calipers. Harvest size frequencies were converted to yield in grams (or kilograms) using seasonal length-wet weight relationships. Male and female exploitation rates were derived from the recapture of marked individuals during the harvest (Ricker 1975). Average catch per unit of effort (CPUE) was computed from the total number and total weight of harvested male and female crayfish.

From sequential population estimates sex-specific fishing mortality rates (F) were calculated (Ricker 1975). These were compared with exploitation rates to evaluate possible trap selectivity bias.

The fishing mortality rate (F) is commonly assumed to be directly proportional to fishing effort (f):

$$F = qf$$

Table 1. Mean daily size (carapace length in mm) of male, female and combined sexes, and recaptured marked crayfish in Dock Lake harvests 1977-1985.

TABLE 1. Mean daily size (carapace length in mm) of male, female and combined sexes, and recaptured marked crayfish in Dock Lake harvests 1977-1985.

		Male			Female			Total		
Day of Harvest		Mean CL (mm)	SE	n	Mean CL (mm)	SE	n	Mean CL (mm)	SE	n
	1	33.2	0.45	35	31.4	0.36	16	32.6	0.35	51
	2	34.0	0.41	39	32.4	0.59	11	33.7	0.36	50
1977	3	33.2	0.38	30	32.4	0.59	16	32.9	0.32	46
	4	33.6	0.43	19	32.3	0.56	12	33.1	0.35	31
	5	34.0	1.09	12	31.3	0.42	7	33.0	0.76	19
Total		33.6	0.22	135	32.0	0.24	62	33.1	0.17	197
	1	33.0	0.25	179	31.4	0.33	121	32.4	0.21	300
	2	32.3	0.35	84	29.8	0.44	66	31.2	0.29	150
1978	3	33.0	0.31	125	30.6	0.43	72	32.1	0.27	197
	4	32.3	0.32	105	30.8	0.36	84	31.6	0.24	189
	5[1]	32.6	0.27	170	30.4	0.35	129	31.7	0.22	299
	6	32.5	0.31	123	29.8	0.33	98	31.3	0.24	221
	7	31.5	0.38	82	29.8	0.49	66	30.8	0.31	148
Total		32.6	0.12	868	30.4	0.14	636	31.7	0.09	1504
	1[1]	32.0	0.41	119	28.9	0.32	97	30.6	0.29	216
	2	31.9	0.45	70	29.3	0.39	79	30.5	0.32	149
1979	3	32.2	0.64	51	28.1	0.57	47	30.2	0.47	98
	4	31.6	0.67	39	29.0	0.48	53	30.1	0.41	92
	5	31.3	0.75	28	29.0	0.78	25	30.2	0.56	53
	6[1]	30.8	0.36	86	29.0	0.40	80	30.0	0.28	166
	7	32.5	0.51	58	29.8	0.47	65	31.1	0.37	123
	8	31.0	0.44	38	28.6	0.47	40	29.8	0.35	78
	9	31.4	0.81	30	28.9	0.51	49	29.9	0.46	79
Total		31.7	0.18	519	29.0	0.15	535	30.3	0.12	1054

TABLE 1. (Cont'd)

Day of Harvest		Male Mean CL (mm)	Male SE	Male n	Female Mean CL (mm)	Female SE	Female n	Total Mean CL (mm)	Total SE	Total n
1979										
Unmarked		31.1	0.18	404	28.6	0.16	462			
Recaptured		33.8	0.41	115	31.5	0.42	73			
	1^{2}	35.2	0.24	197	32.4	0.32	108	34.2	0.21	305
	2	33.6	0.26	116	31.3	0.38	84	32.6	0.23	200
1980	3	33.4	0.49	44	31.3	0.36	52	32.3	0.32	96
	4	34.5	0.49	52	31.4	0.51	44	33.1	0.38	96
	5^{1}	33.3	0.28	93	32.1	0.38	89	32.7	0.24	182
	6	33.2	0.46	59	31.6	0.35	45	32.5	0.31	104
	7	33.0	0.57	36	31.2	0.46	32	32.2	0.38	68
	8	33.5	0.46	47	32.4	0.40	55	32.9	0.30	102
Total		34.0	0.13	644	31.8	0.14	509	33.0	0.10	1153
	1	35.1	0.31	82	33.6	0.39	70	34.4	0.25	152
	2	34.9	0.43	43	33.0	0.40	43	33.9	0.31	86
1981	3	34.3	0.36	33	33.1	0.72	24	33.8	0.37	57
	4^{1}	34.6	0.27	120	32.7	0.26	98	33.8	0.20	218
	5	34.8	0.47	40	32.6	0.32	43	33.6	0.30	83
	6	33.2	0.66	16	33.5	0.68	29	33.4	0.49	45
	7	33.9	0.46	52	32.1	0.41	60	33.0	0.32	112
	8	34.9	0.65	21	33.3	0.53	30	34.0	0.42	51
	9^{1}	34.2	0.31	81	31.7	0.41	57	33.2	0.27	138
Total		34.5	0.13	488	32.8	0.14	454	33.7	0.10	942
Unmarked		34.0	0.15	310	32.5	0.16	358			
Recaptured		35.4	0.23	178	33.8	0.28	96			

TABLE 1. (Cont'd.)

		Male			Female			Total		
Day of Harvest		Mean CL (mm)	SE	n	Mean CL (mm)	SE	n	Mean CL (mm)	SE	n
	1[1]	34.9	0.21	279	31.7	0.32	127	33.9	0.19	406
	2	33.9	0.27	163	31.3	0.28	134	32.7	0.21	297
	3	33.8	0.43	62	31.0	0.41	59	32.4	0.32	121
	4	33.6	0.48	74	31.3	0.41	72	32.5	0.33	146
	5	34.0	0.40	64	31.2	0.37	66	32.6	0.30	130
	6[1]	33.6	0.23	203	31.8	0.28	130	32.9	0.18	333
1982	7	32.9	0.28	133	31.4	0.28	135	32.1	0.20	268
	8	32.8	0.45	48	31.0	0.50	52	31.9	0.35	100
	9	33.2	0.49	52	31.8	0.42	59	32.4	0.33	111
	10	32.2	0.50	38	32.0	0.55	43	32.1	0.37	81
	11[1]	33.3	0.28	150	32.0	0.36	98	32.8	0.22	248
	12	32.6	0.38	77	32.1	0.40	87	32.3	0.28	164
	13	32.8	0.44	38	32.8	0.66	31	32.8	0.38	69
	14	33.0	0.37	65	31.1	0.50	45	32.2	0.31	110
Total		33.6	0.09	1146	31.6	0.10	1138	32.7	0.07	2584
Unmarked		33.2	0.10	1041	31.4	0.11	958			
Recaptured		34.8	0.19	405	32.6	0.26	180			
	1[1]	34.8	0.22	348	31.9	0.34	134	34.0	0.19	482
	2	33.5	0.24	241	31.6	0.31	165	32.8	0.20	406
	3	32.6	0.33	136	30.8	0.37	111	31.8	0.25	247
	4	32.8	0.30	146	30.4	0.36	107	31.8	0.24	253
	5	32.8	0.26	169	31.0	0.37	139	32.0	0.23	308
	6[1]	32.5	0.20	298	30.7	0.27	235	31.7	0.17	533
1983	7	31.7	0.33	131	30.7	0.30	148	31.1	0.22	279
	8	31.4	0.26	97	30.2	0.34	105	30.8	0.22	202
	9	32.5	0.37	94	31.9	0.49	72	32.3	0.30	166
	10	32.0	0.28	99	30.5	0.41	81	31.3	0.25	180
	11[1]	32.3	0.27	170	30.4	0.32	131	31.5	0.21	301
	12	31.6	0.40	79	30.6	0.40	84	31.1	0.29	163
	13	31.0	0.38	63	30.2	0.48	68	30.6	0.31	131

TABLE 1. (Cont'd)

Day of Harvest	Male			Female			Total		
	Mean CL (mm)	SE	n	Mean CL (mm)	SE	n	Mean CL (mm)	SE	n
1983(cont'd)									
14	32.2	0.39	61	29.7	0.44	59	31.0	0.31	120
Total	32.8	0.08	2132	30.8	0.10	1639	32.0	0.06	3771
Unmarked	32.3	0.08	1648	30.5	0.10	1342			
Recaptured	34.5	0.19	484	32.5	0.24	297			
1	35.2	0.29	244	31.1	0.33	110	33.9	0.25	354
2	34.6	0.31	198	31.6	0.33	119	33.5	0.24	317
3[1]	34.7	0.22	334	31.8	0.28	172	33.7	0.18	506
4	33.6	0.29	174	31.6	0.39	93	32.9	0.24	267
5	32.8	0.34	118	31.1	0.46	68	32.2	0.28	186
6	32.8	0.31	100	31.0	0.38	78	32.0	0.25	178
1984 7	32.7	0.39	85	31.3	0.49	55	32.1	0.31	140
8[1]	32.7	0.21	294	31.6	0.31	151	32.3	0.18	445
9	32.3	0.28	128	30.4	0.39	80	31.6	0.24	208
10	32.3	0.38	90	30.4	0.42	70	31.5	0.29	160
11	31.3	0.34	79	31.2	0.42	61	31.2	0.26	140
12	31.1	0.32	67	30.9	0.43	62	31.0	0.26	129
13[3]	32.4	0.90	11	32.2	1.16	9	32.3	0.70	20
Total	33.5	0.09	1922	31.3	0.11	1128	32.7	0.07	3050
Unmarked	32.4	0.10	1284	31.0	0.11	919			
Recaptured	35.7	0.17	638	32.7	0.27	209			
1[2]	34.2	0.26	337	29.0	0.29	143	32.6	0.23	480
2	32.1	0.28	253	29.4	0.25	171	31.0	0.21	424
3	30.7	0.31	147	29.8	0.30	125	30.3	0.22	272

TABLE 1. (Cont'd)

Day of Harvest	Male Mean CL (mm)	Male SE	Male n	Female Mean CL (mm)	Female SE	Female n	Total Mean CL (mm)	Total SE	Total n
4	31.4	0.40	130	29.0	0.34	128	30.2	0.27	258
5[1]	31.8	0.27	294	29.6	0.27	168	31.0	0.20	462
6	31.8	0.25	256	30.2	0.26	164	31.2	0.19	420
7	31.6	0.30	150	29.4	0.30	126	30.6	0.22	276
8	31.8	0.35	138	29.3	0.33	117	30.6	0.25	255
9	31.4	0.36	119	28.8	0.41	92	30.3	0.28	211
1985 10[1]	31.5	0.24	312	29.2	0.27	170	30.7	0.19	482
11	30.5	0.26	146	29.8	0.34	133	30.2	0.21	279
12	30.4	0.35	90	28.7	0.42	66	29.7	0.27	156
13	31.3	0.37	94	29.1	0.44	62	30.4	0.30	156
14	30.2	0.43	58	28.8	0.43	56	29.5	0.31	114
15[1]	31.0	0.22	237	30.1	0.33	128	30.7	0.18	365
16	30.4	0.20	144	29.7	0.29	117	30.1	0.17	261
17	30.0	0.37	81	29.7	0.51	74	29.9	0.31	155
18	30.6	0.43	58	30.0	0.54	54	30.3	0.34	112
19	30.4	0.28	69	29.1	0.44	66	29.8	0.26	135
20[4]	30.8	0.25	171	28.8	0.31	114	30.0	0.20	285
Total	31.5	0.07	3284	29.4	0.07	2274	30.7	0.05	5558
Unmarked	30.8	0.07	2514	29.0	0.08	1864			
Recaptured	33.9	0.16	770	31.3	0.20	410			

[1] Three day harvest

[2] Four day harvest

[3] Harvest from 16 traps

[4] Two day harvest

The constant of proportionality **q** is called the catchability coefficient, the proportion of the stock removed by one unit of nominal fishing effort (Ricker 1975). This assumption allows for estimation of stock abundance from changes in CPUE, and transforms the biological variables of growth, mortality and recruitment into catch (Rothschild 1977). However variations in q resulting from gear selectivity, gear saturation or density dependence could provide misleading appraisals of abundance. Possible departures from this simple assumption were evaluated for male and female crayfish at varying fishing efforts, sampling intensities and population densities.

Variations in mean size of harvested crayfish were detected by analysis of variance with **a posteriori** analysis of significant differences by the Scheffe method, alpha level = 0.05. Differences in age- and sex-specific ratios between the crayfish population and those harvested in Dock Lake were evaluated with chi-square tests (Zar 1974). Regression analysis tested the relationships between variables.

RESULTS

Assessment of the Crayfish Fishery

Size composition samples were examined to investigate possible annual fluctuations in mean size. Harvested male crayfish were always significantly larger ($P<0.0001$) than female crayfish regardless of effort (Table 1). The mean size of male and female crayfish harvested in 1979 and 1985 were smaller ($P<0.05$) than all other years. The largest crayfish were harvested in 1981 (Table 1).

Table 2. Proportion of male and female crayfish less than or equal to 30 mm carapace length harvested in Dock Lake 1977-1985.

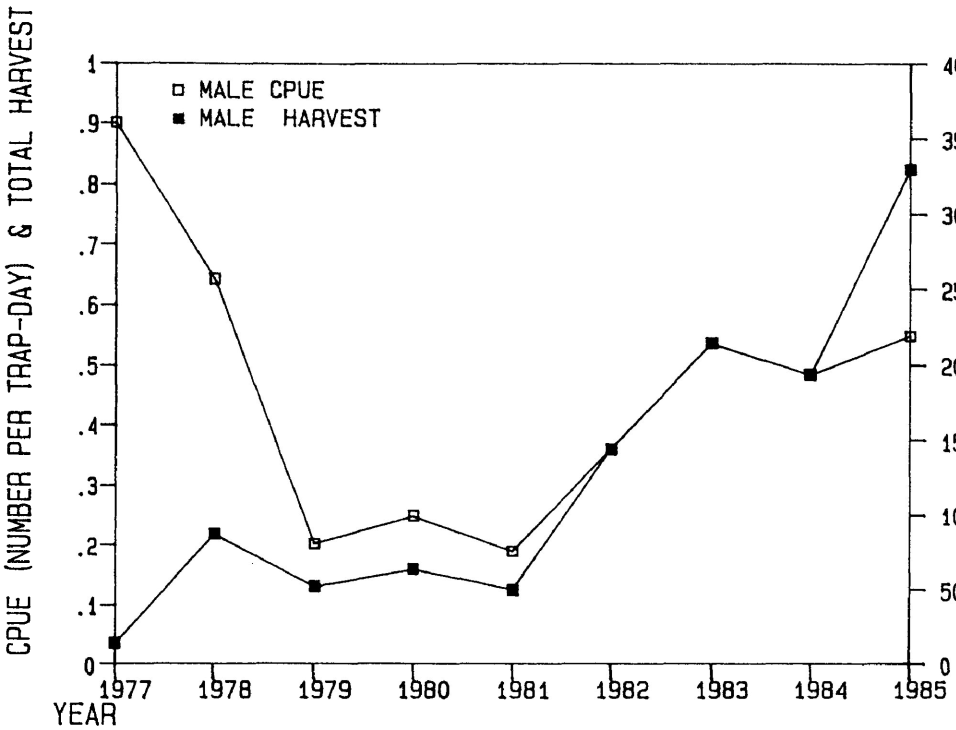
TABLE 2. Proportion of male and female crayfish less than or equal to 30 mm and greater than 30 mm carapace length harvested in Dock Lake 1977-1985.

Carapace	1977				1978				1979			
Length	M		F		M		F		M		F	
(mm)	#	%	#	%	#	%	#	%	#	%	#	%
≤ 30	19	14.1	15	24.2	243	28.0	328	51.6	230	44.3	377	70.5
> 30	116	85.9	47	75.8	625	72.0	308	48.4	289	55.7	158	29.5

Carapace	1980				1981				1982			
Length	M		F		M		F		M		F	
(mm)	#	%	#	%	#	%	#	%	#	%	#	%
≤ 30	81	12.6	165	32.4	30	6.1	108	23.8	244	16.9	442	38.8
> 30	563	87.4	344	67.6	458	93.9	346	76.2	1202	83.1	696	61.2

Carapace	1983				1984				1985			
Length	M		F		M		F		M		F	
(mm)	#	%	#	%	#	%	#	%	#	%	#	%
≤ 30	585	27.4	864	52.7	452	23.5	519	46.0	1494	45.5	1480	65.1
> 30	1547	72.6	775	47.3	1470	76.5	609	54.0	1790	54.5	794	34.9

Figure 1. Male and female catch-per-unit-effort (CPUE) in number harvested per trap-day and total number harvested for nominal efforts of 150 to 6000 trap-days.


CPUE (NUMBER PER TRAP-DAY) & TOTAL HARVEST
□ MALE CPUE
■ MALE HARVEST
1
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
4000
3500
3000
2500
2000
1500
1000
500
0
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

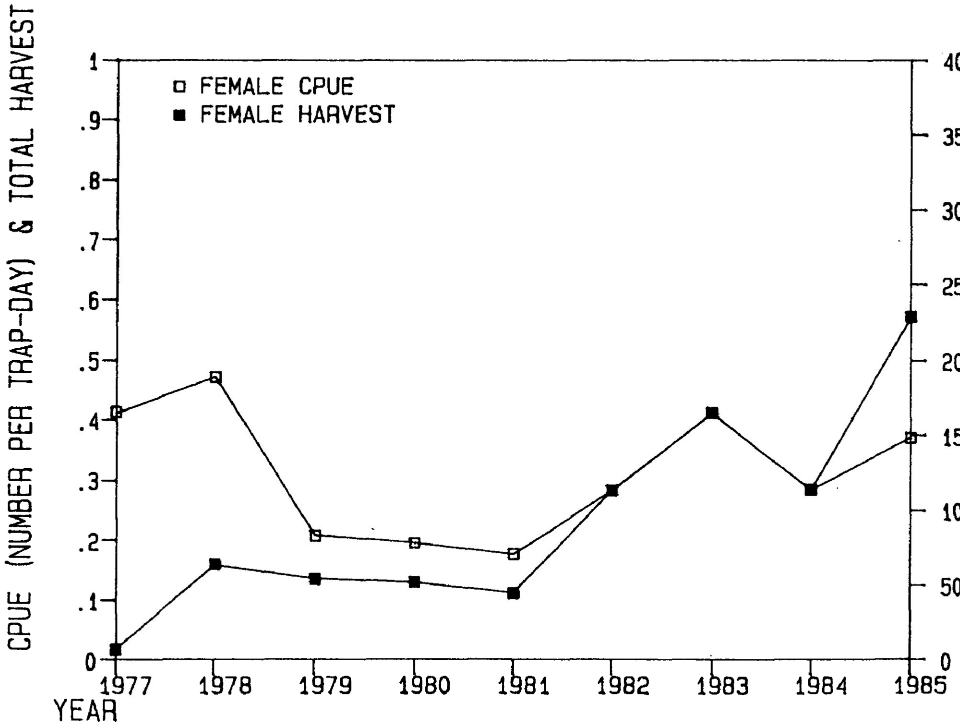
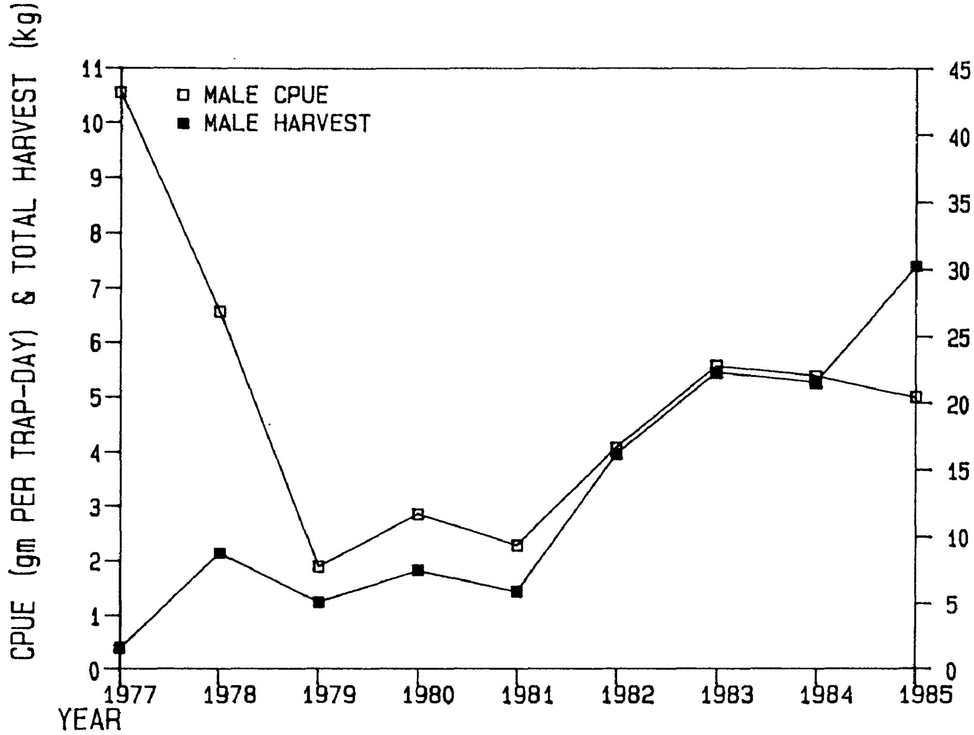
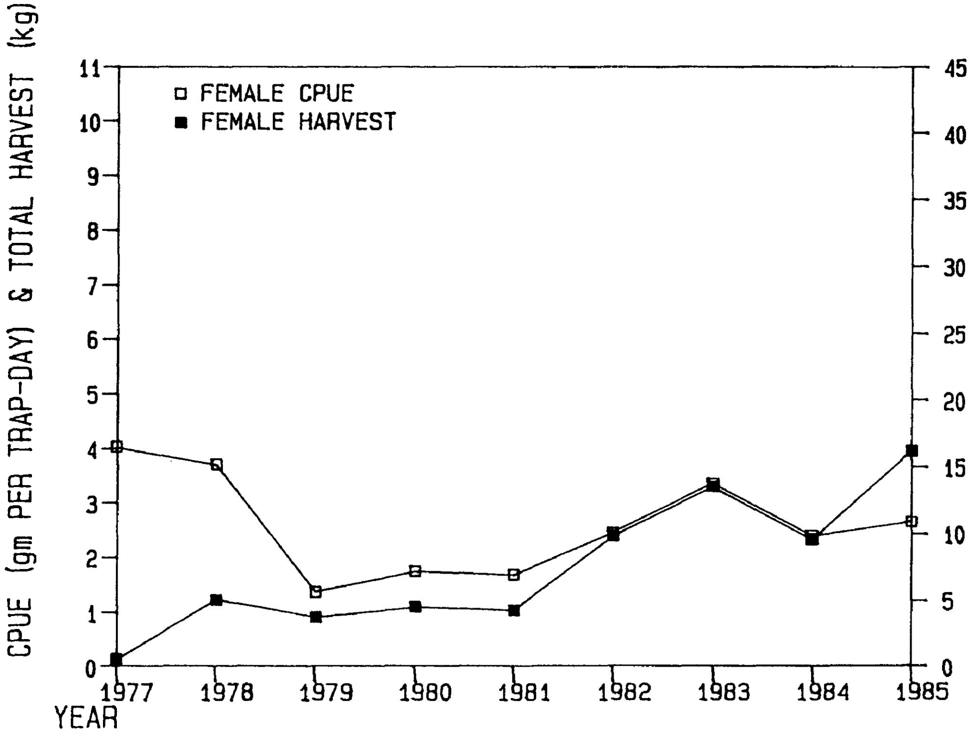

CPUE (NUMBER PER TRAP-DAY) & TOTAL HARVEST
□ FEMALE CPUE
■ FEMALE HARVEST
1
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
4000
3500
3000
2500
2000
1500
1000
500
0
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

Figure 2. Male and female catch-per-unit-effort (CPUE) in weight (gm) harvested per trap-day and total weight harvested in kilograms for nominal efforts of 150 to 6000 trap-days.



CPUE (gm PER TRAP-DAY) & TOTAL HARVEST (kg)
□ MALE CPUE
■ MALE HARVEST
0
1
2
3
4
5
6
7
8
9
10
11
0
5
10
15
20
25
30
35
40
45
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR



CPUE (gm PER TRAP-DAY) & TOTAL HARVEST (kg)
□ FEMALE CPUE
■ FEMALE HARVEST
0
1
2
3
4
5
6
7
8
9
10
11
0
5
10
15
20
25
30
35
40
45
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

Intra-annual variation in male and female mean daily size was independent from 1977 to 1981 (Table 1). Male mean daily size decreased ($P<0.0005$) during the harvest at nominal efforts of 4000 trap-days and greater but female size declined ($P<0.006$) only during the 1983 harvest. For combined sexes, mean daily size decreased during the harvests of 1981 ($P<0.03$) and 1983-85 ($P<0.0005$).

Small crayfish <30 mm C.L. constitute a variable proportion of the catch both between sexes and between years (Table 2). Regardless of nominal effort females always constituted a greater percentage of these small individuals. By increasing effort from 150 to 1350 trap-days we doubled the proportion of small crayfish in the harvest. From 1978 to 1979 effort almost doubled and the percentage of small crayfish harvested increased 1.5 times. Though effort remained constant at 2600 trap-days from 1979-1981 the relative amount of small crayfish in the catch declined (Table 2). Increasing the effort approximately 1.5 times to 4000 trap-days stabilized the percent harvest of small crayfish. At 6000 trap-days small crayfish dominated the catch.

The catch per unit of effort (CPUE), expressed as the number or weight of crayfish per trap-day, declined from 1977 to 1979 with increases in fishing effort (Fig. 1 and 2). From 1979 to 1981 CPUE and effort remained constant. CPUE increased two-to-threefold at nominal efforts of 4000 trap-days from 1982 to 1984. A similar concordant CPUE occurred in 1985 (i.e., similar to CPUE at 4000 trap-days) although nominal effort increased to 6000 trap-days. The trend in CPUE was similar between the sexes (Fig. 1 and 2).

The total annual harvest was proportional to nominal effort (Fig. 1 and 2). However the interaction between fishing effort and sampling intensity profoundly changed CPUE and total catch relationships between years. At efforts of 150 and 1350 trap-days CPUE decreased independently of annual harvest. From 1979 to 1981 constant effort resulted in a consistent CPUE-annual harvest relationship. However the 1979-81 CPUE was higher than expected on the basis of population density (i.e., stable CPUE at decreasing population density). CPUE and total annual harvest were proportional from 1982-84 at an effort of 4000 trap-days. Increasing the effort to 6000 trap-days in 1985 produced lower CPUE than expected even though yield increased (Fig. 1 and 2).

Increasing fishing effort changed susceptibility of crayfish to the gear. At efforts of 150 and 1350 trap-days, a significantly higher CPUE indicates greater vulnerability. This is the result of changing sampling intensity (i.e., 50 traps in 1978 and 150 traps in 1979). Gear saturation takes place at about 200 traps. This is inferred from the consistently higher then expected 1979-1981 CPUE which was then followed by the proportional relationship between 1982-1984 CPUE and annual harvest. However the differences between the 1979-81, 1982-84 and 1985 periods indicates decreased vulnerabilities as harvest duration increased (i.e., from 1979-85 the number of sampling units remained the same, only the number of days increased). In 1984 use of 250 traps decreased total harvest and CPUE. This resulted from gear competition whereby the fraction of the population taken by a single unit of nominal effort decreased,

Table 3. Day of harvest when 50% of the total male and female yield was caught in Dock Lake 1977-1985.

TABLE 3. Day of harvest when 50% of the total male and female yield was caught in Dock Lake, 1977-1985.

Year	Sex	Day of 50% of Total Harvest	% of Total Number of Days	Effort in Trap-Days	Number of Days
1977	M	2.511	50.22	150	5
	F	2.726	54.22	(1000)	(5)
1978	M	3.806	42.29	1350	9
	F	3.931	43.68	(1800)	(7)
1979	M	6.247	48.05	2600	13
	F	6.540	50.31		(9)
1980	M	6.441	49.55	2600	13
	F	6.904	53.11		(8)
1981	M	6.721	51.70	2600	13
	F	6.806	52.35		(9)
1982	M	10.062	50.31	4000	20
	F	10.544	52.72		(14)
1983	M	9.851	49.26	4000	20
	F	10.603	53.02		(14)
1984	M	7.381	46.13	4000	16
	F	7.841	49.01	(3200)	(13)
1985	M	12.796	42.65	6000	30
	F	13.210	44.03		(20)

Table 4. Daily proportion of age- and sex-specific male and female crayfish harvested in Dock Lake 1977-1985.

TABLE 4. Daily proportion of age- and sex-specific male and female crayfish harvested in Dock Lake 1977-1985.

Day of Harvest		I				II				III			
		M		F		M		F		M		F	
		#	%	#	%	#	%	#	%	#	%	#	%
1977	1	24	47.1	12	23.5	11	21.6	4	7.8				
	2	22	44.0	6	12.0	17	34.0	5	10.0				
	3	23	50.0	10	21.7	7	15.2	6	13.0				
	4	14	45.2	8	25.8	5	16.1	4	12.9				
	5	6	31.6	6	31.6	5	26.3	1	5.3	1	5.3		
	$\bar{X}$		43.58		22.92		22.64		9.80		1.06		
	S.D.		7.07		7.15		7.77		3.32		2.37		
1978	1	126	42.0	61	20.3	52	17.3	56	18.7	1	0.3	4	1.3
	2	68	45.3	45	30.0	16	10.7	21	14.0				
	3	90	45.7	47	23.9	35	17.8	23	11.7			2	1.0
	4	78	41.3	53	28.0	27	14.3	29	15.3			2	1.1
	5[1]	119	39.8	79	26.4	51	17.1	47	15.7			3	1.0
	6	93	42.1	69	31.2	30	13.6	29	13.1				
	7	68	45.9	43	29.0	14	9.5	22	14.9			1	0.7
	$\bar{X}$		43.16		26.97		14.33		14.77		0.04		0.73
	S.D.		2.44		3.80		3.31		2.21		0.11		0.53
1979	1[1]	81	37.5	48	22.2	36	16.7	49	22.7	2	0.9		
	2	50	33.6	31	20.8	20	13.4	44	29.5			4	2.7
	3	31	31.6	29	29.6	20	20.4	16	16.3			2	2.0
	4	29	31.5	28	30.4	10	10.9	22	23.9			3	3.3
	5	22	41.5	11	20.8	5	9.4	14	26.4	1	1.9		
	6[1]	70	42.2	39	23.5	16	9.6	40	24.1			1	0.6
	7	39	31.7	27	22.0	19	15.4	35	28.5			3	2.4
	8	32	41.0	19	24.4	6	7.7	21	26.9				
	9	23	29.1	23	29.1	7	8.9	25	31.6			1	1.3
	$\bar{X}$		35.52		24.76		12.49		25.54		0.31		1.37
	S.D.		5.07		3.89		4.27		4.50		0.67		1.28
1980	1[2]	116	38.0	70	23.0	75	24.6	37	12.1	6	2.0	1	0.3
	2	87	43.5	63	31.5	29	14.5	19	9.5			2	1.0
	3	34	35.4	42	43.8	9	9.4	9		1	1.0	1	1.0
	4	34	35.4	34	35.4	17	17.7	9	9.4	1	1.0	1	1.0
	5[1]	76	41.8	62	34.1	17	9.3	23	12.6			4	2.2
	6	49	47.1	34	32.7	8	7.7	11	10.6	2	1.9		
	7	30	44.1	27	39.7	5	7.4	5	7.4	1	1.5		
	8	37	36.3	35	34.3	9	8.8	20	19.6	1	1.0		
	$\bar{X}$		40.20		34.31		12.42		11.32		1.05		0.69
	S.D.		4.51		6.08		6.09		3.73		0.76		0.77

TABLE 4. (Cont'd)

Day of Harvest		I				II				III			
		M		F		M		F		M		F	
		#	%	#	%	#	%	#	%	#	%	#	%
1981	1	35	23.0	21	13.8	42	27.6	44	28.9	5	3.3	5	3.3
	2	22	25.6	21	24.4	18	20.9	21	24.4	3	3.5	1	1.2
	3	17	29.8	11	19.3	16	28.1	11	19.3			2	3.5
	4[1]	64	29.4	49	22.5	46	21.1	47	21.6	10	4.6	2	0.9
	5	17	20.5	21	25.3	22	26.5	22	26.5	1	1.2		
	6	10	22.2	13	28.9	6	13.3	13	28.9			3	6.7
	7	31	27.7	33	29.5	16	14.3	27	24.1	5	4.5		
	8	10	19.6	12	23.5	8	15.7	16	31.4	3	5.9	2	3.9
	9[1]	52	37.7	33	23.9	23	16.7	22	15.9	6	4.3	2	1.4
	X̄		26.17		23.46		20.47		24.56		3.03		2.32
	S.D.		5.70		4.77		5.84		5.00		2.14		2.21
1982	1[1]	185	45.6	78	19.2	83	20.4	45	11.1	11	2.7	4	1.0
	2	124	41.8	93	31.3	39	31.1	38	12.8			3	1.0
	3	49	40.5	41	33.9	11	9.1	18	14.9	2	1.6		
	4	57	39.0	47	32.2	15	10.3	23	15.8	2	1.4	2	1.4
	5	51	39.2	48	36.9	12	9.2	17	13.1	1	0.8	1	0.8
	6[1]	168	50.5	77	23.1	31	9.3	51	15.3	4	1.2	2	0.6
	7	118	44.0	86	32.1	13	4.9	48	17.9	2	0.7	1	0.4
	8	42	42.0	33	33.0	6	6.0	19	19.0				
	9	44	39.6	31	27.9	7	6.3	27	24.3	1	0.9	1	0.9
	10	34	42.0	26	32.1	4	4.9	15	18.5			2	2.5
	11[1]	123	49.6	57	23.0	25	10.1	40	16.1	2	0.8	1	0.4
	12	67	40.9	49	29.9	8	4.9	35	21.3	2	1.2	3	1.8
	13	35	50.7	15	21.7	3	4.4	15	21.7			1	1.4
	14	58	52.7	29	26.4	6	5.5	16	14.5	1	0.9		
	X̄		44.15		28.76		8.46		16.88		0.87		1.13
	S.D.		4.79		5.30		4.35		3.76		0.76		1.09
1983	1[1]	213	44.2	92	19.1	118	24.5	36	7.5	17	3.5	6	1.2
	2	181	44.6	120	29.6	54	13.3	34	8.4	6	1.5	11	2.7
	3	111	44.9	85	34.4	23	9.3	21	8.2	2	0.8	5	2.0
	4	115	45.4	84	33.2	28	11.1	19	7.5	3	1.2	4	1.6
	5	139	45.1	102	33.1	27	8.8	27	8.8	3	1.0	10	3.2
	6[1]	246	46.1	180	33.8	50	9.4	44	8.3	2	0.4	11	2.1
	7	115	41.2	116	41.6	15	5.4	29	10.4	1	0.4	3	1.1
	8	91	45.0	89	44.1	6	3.0	13	6.4			3	1.5
	9	79	47.6	50	30.1	14	8.4	15	9.0	1	0.6	7	4.2
	10	93	51.7	64	35.6	5	2.8	16	8.9	1	0.5	1	0.5
	11[1]	143	47.5	109	36.2	26	8.6	18	6.0	1	0.3	4	1.3
	12	70	42.9	64	39.3	9	5.5	19	11.7			1	0.6
	13	60	45.8	52	39.7	3	2.3	14	10.7			2	1.5
	14	53	44.2	51	42.5	8	6.7	7	5.8			1	0.8
	X̄		45.44		35.16		8.51		8.42		0.73		1.74
	S.D.		2.44		6.44		5.62		1.73		0.93		1.04

TABLE 4. (Cont'd)

Day of Harvest		I				II				III			
		M		F		M		F		M		F	
		#	%	#	%	#	%	#	%	#	%	#	%
1984	1	154	43.5	58	16.4	74	20.9	50	14.1	16	4.5	2	0.6
	2	133	42.0	68	21.4	57	18.0	44	13.9	8	2.5	7	2.2
	3[1]	230	45.4	89	17.6	93	18.4	72	14.2	11	2.2	11	2.2
	4	136	50.9	53	19.9	35	13.1	35	13.1	3	1.1	5	1.9
	5	98	52.7	41	22.0	20	10.8	23	12.4			4	2.1
	6	91	51.1	45	25.3	8	4.5	30	16.8	1	0.6	3	1.7
	7	73	52.1	32	22.9	11	7.9	21	15.0	1	0.7	2	1.4
	8[1]	238	53.5	76	17.1	55	12.4	67	15.0	1	0.2	8	1.8
	9	111	53.4	54	26.0	17	8.2	24	11.5			2	1.0
	10	76	47.5	46	28.8	14	8.8	22	13.8			2	1.2
	11	75	53.6	34	24.3	4	2.8	26	18.6			1	0.7
	12	65	50.4	38	29.4	2	1.6	22	17.0			2	1.6
	13[3]	10	50.0	4	20.0	1	5.0	5	25.0				
	$\bar{X}$		49.70		22.39		10.18		15.42		0.91		1.42
	S.D.		3.91		4.24		6.16		3.47		1.38		0.68
1985	1[2]	157	32.7	98	20.4	169	35.2	42	8.8	11	2.3	3	0.6
	2	176	41.5	112	26.4	75	17.7	59	13.9	2	0.5		
	3	116	42.6	74	27.2	30	11.0	51	18.8	1	0.4		
	4	93	36.0	88	34.1	35	13.6	39	15.1	2	0.8	1	0.4
	5[1]	197	42.6	108	23.4	94	20.3	57	12.3	3	0.7	3	0.7
	6	181	43.1	86	20.5	72	17.1	77	18.3	3	0.7	1	0.2
	7	113	40.9	78	28.3	35	12.7	48	17.4	2	0.7		
	8	95	37.2	81	31.8	42	16.5	34	13.3	1	0.4	2	0.8
	9	89	42.2	65	30.8	27	12.8	26	12.3	3	1.4	1	0.5
	10[1]	231	47.9	116	24.1	77	16.0	51	10.6	4	0.8	3	0.6
	11	130	46.6	80	28.7	16	5.7	49	17.6			4	1.4
	12	75	48.1	49	31.4	15	9.6	16	10.3			1	0.6
	13	71	45.5	45	28.8	22	14.1	16	10.3	1	0.6	1	0.6
	14	53	46.5	41	36.0	5	4.4	15	13.2				
	15[1]	200	54.8	77	21.1	34	9.3	47	12.9	3	0.8	4	1.1
	16	134	51.3	73	28.0	10	3.8	44	16.9				
	17	73	47.1	47	30.3	8	5.2	25	16.1			2	1.3
	18	52	46.4	32	28.6	5	4.5	19	17.0	1	0.9	3	2.7
	19	64	47.4	49	36.3	5	3.7	15	11.1			2	1.5
	20	148	51.9	81	28.4	22	7.7	33	11.6	1	0.4		
	$\bar{X}$		44.62		28.23		12.04		13.89		0.57		0.65
	S.D.		5.43		4.65		7.53		3.05		0.56		0.69

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[1] Three day harvest

[2] Four day harvest

[3] Harvest from 16 traps

[4] Two day harvest

Table 5. Dock Lake age- and sex-specific population density and harvest structure from 1976-1985.

TABLE 5. Dock Lake age- and sex-specific population density and harvest structure from 1976-1985.

Year	Age		Male				Female					Total	
	Class	N	%	Harvest	%	N	%	Harvest	%	N	%	Harvest	:%
1976	I	609	33.2			627	34.2			1236	67.4		
	II	268	14.6			294	16.0			562	30.6		
	III	8	0.4			29	1.6			37	2.0		
	Total	885	48.2			950	51.8			1835	100.0		
1977	I	958	36.4	89	45.2	949	36.1	42	21.3	1907	72.5	131	66.5
	II	383	14.6	45	22.8	299	11.4	20	10.2	682	26.0	65	33.0
	III	27	1.0	1	0.5	14	0.5	0	0	41	1.5	1	0.5
	Total	1368	52.0	135	68.5	1262	48.0	62	31.5	2630	100.0	197	100.0
1978	I	1260	29.1	642	42.7	1503	34.7	397	26.4	2763	63.8	1039	69.1
	II	796	18.4	225	15.0	724	16.7	227	15.1	1520	35.1	452	30.1
	III	8	0.2	1	0.1	43	1.0	12	0.8	51	1.2	13	0.9
	Total	2064	47.7	868	57.8	2270	52.4	636	42.3	4334	100.1	1504	100.1
1979	I	934	31.1	377	35.8	1013	33.7	255	24.2	1947	64.8	632	60.0
	II	469	15.6	139	13.2	533	17.7	266	25.2	1002	33.3	405	38.4
	III	17	0.6	3	0.3	39	1.3	14	1.3	56	1.9	17	1.6
	Total	1420	47.3	519	49.3	1585	52.7	535	50.7	3005	100.0	1054	100.0
1980	I	932	36.6	463	40.2	947	37.2	367	31.8	1879	73.8	830	72.0
	II	336	13.2	169	14.7	286	11.2	133	11.5	622	24.4	302	26.2
	III	33	1.3	12	1.0	9	0.4	9	0.8	42	1.7	21	1.8
	Total	1301	51.1	644	55.9	1242	48.8	509	44.1	2543	99.9	1153	100.0
1981	I	629	23.4	258	27.4	951	35.3	214	22.7	1580	58.7	472	50.1
	II	469	17.4	197	20.9	580	21.5	223	23.7	1049	38.9	420	44.6
	III	33	1.2	33	3.5	30	1.1	17	1.8	63	2.3	50	5.3
	Total	1131	42.0	488	51.8	1561	57.9	454	48.2	2692	99.9	942	100.0

TABLE 5. (Cont'd)

Year	Age Class	Male				Female				Total			
		N	%	Harvest	%	N	%	Harvest	%	N	%	Harvest	%
1982	I	1650	38.4	1155	44.7	1463	34.0	710	27.5	3113	72.4	1865	72.2
	II	371	8.6	263	10.2	737	17.1	407	15.8	1108	25.7	670	26.0
	III	39	0.9	28	1.1	40	0.9	21	0.8	79	1.8	49	1.9
	Total	2060	47.9	1446	56.0	2240	52.0	1138	44.1	4300	99.9	2584	100.1
1983	I	2402	36.8	1709	45.3	2736	41.9	1258	33.4	5138	78.7	2967	78.7
	II	495	7.6	386	10.2	738	11.3	312	8.3	1233	18.9	698	18.5
	III	88	1.3	37	1.0	75	1.1	69	1.8	163	2.4	106	2.8
	Total	2985	45.7	2132	56.5	3549	54.3	1639	43.5	6534	100.0	3771	100.0
1984	I	2606	37.5	1490	48.8	2157	31.0	638	20.9	4763	68.5	2128	69.7
	II	693	10.0	391	12.8	1290	18.6	441	14.5	1983	28.6	832	27.3
	III	56	0.8	41	1.3	147	2.1	49	1.6	203	2.9	90	2.9
	Total	3355	48.3	1922	62.9	3594	51.7	1128	37.0	6949	100.0	3050	99.9
1985	I	3402	36.7	2448	44.0	3445	37.1	1480	26.6	6847	73.8	3928	70.6
	II	970	10.5	798	14.4	1383	14.9	763	13.7	2353	25.4	1561	28.1
	III	38	0.4	38	0.7	35	0.4	31	0.6	73	0.8	69	1.3
	Total	4410	47.6	3284	59.1	4863	52.4	2274	40.9	9273	100.0	5558	100.0

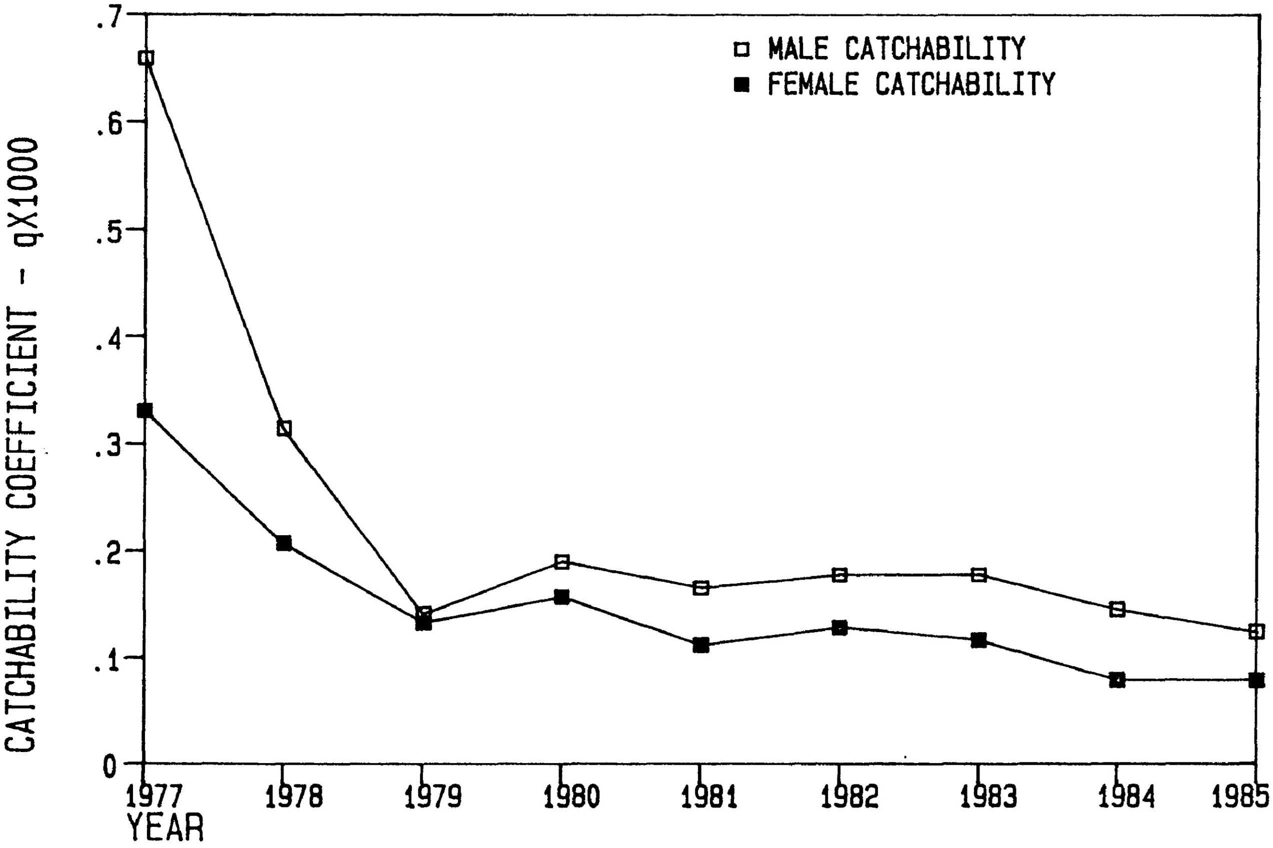
which in turn reduced total harvest (Rothschild 1977).

Daily age- and sex-specific harvests varied little over nine years (Tables 3 and 4). Generally, 50% of the males were caught midway through the harvest (Table 3). The females reached 50% harvest levels one day later. Slight differences occurred when the midpoint of the harvest extended over a weekend period (1978 and 1984). The decline in daily CPUE at 6000 trap-days effort lowered the 50% harvest midpoint. Although nominal effort has increased 40 times, only at 6000 trap-days was there any symptom of over-harvest. At that level of harvest the catch exhibited: (1) smallest average size of crayfish, (2) high percentage of `small' crayfish, (3) daily decreasing average male size, (4) decreasing daily CPUE and (5) lower CPUE than expected from total harvest.

Exploitation visibly affected the percent harvest of age II male crayfish (Table 4). During the first few days age II males comprised 20-30% of the catch. However by the end of the harvest the percent of age II males declined to less than 10%. This at an effort equal to or exceeding 2600 trap-days. The proportion of age I males and females, and age II females stabilized over the harvest period. Therefore decline in daily catch of age II males allowed increased numbers of age I male and female, and age II female crayfish to enter the traps. This kept daily CPUE relatively constant.

Crayfish generally were harvested in proportion to their age-specific abundance despite marked changes in fishing effort (Table 5). Male crayfish were caught at the same relative frequencies as their age-class abundance for all years except

Figure 3. Time trend of Dock Lake male and female catchability coefficients (q).



□ MALE CATCHABILITY
■ FEMALE CATCHABILITY
CATCHABILITY COEFFICIENT - qX1000
.7
.6
.5
.4
.3
.2
.1
0
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

1978, 1979, 1981, 1983 and 1985 ($P<0.05$). For females, relative harvest frequencies often differed from that of the population (1979, 1980, 1981, 1983 and 1985) ($P<0.05$). Combined male and female harvest frequencies differed from the population age structure in 1978, 1979, 1981 and 1985 ($P<0.025$). However these statistical differences were caused by the disparity between low age III abundance and their high vulnerability to passive fishing gear compared to that of younger age groups (i.e., all age III crayfish were harvested annually). Through removal of crayfish in proportion to their abundance, exploitation stabilized the male and female age structure (Table 5). However because males were more vulnerable to fishing this produced a differential sex ratio ($P<0.01$) between harvested and exploitable stock in all years except 1979 (Table 5).

Differential Density-Dependent Catchability

Changes in age- and sex-specific harvest parameters strongly suggest that catchability varies with sampling intensity, duration of harvest and population density. The interpretation of CPUE data was made more difficult because of these inter-related variables. Their influence on q was separately analysed for males and females.

There was no time series trend in the catchability (q) of males or females (Fig. 3). As sampling intensity increased from 150 to 1350 trap-days catchability of males and females significantly decreased. However at harvest rates of 2600 to 4000 trap-days though male catchability remained relatively constant, female catchability varied. At efforts equal to or exceeding 2600

Figure 4. Relationships between male and female Dock Lake population density and catchability coefficient (q) 1977-1985. Regression line, female: lnY=-0.3662lnX+0.6790, R2=0.69 (P<0.04), for relationship between logarithmically transformed (Napierian logarithm) catchability (qX10-4) (Y) and logarithmically transformed absolute density (X). Regression of similar relationship for males was not significant, q=0.1702x10-4 (standard error=0.0084x10-4.

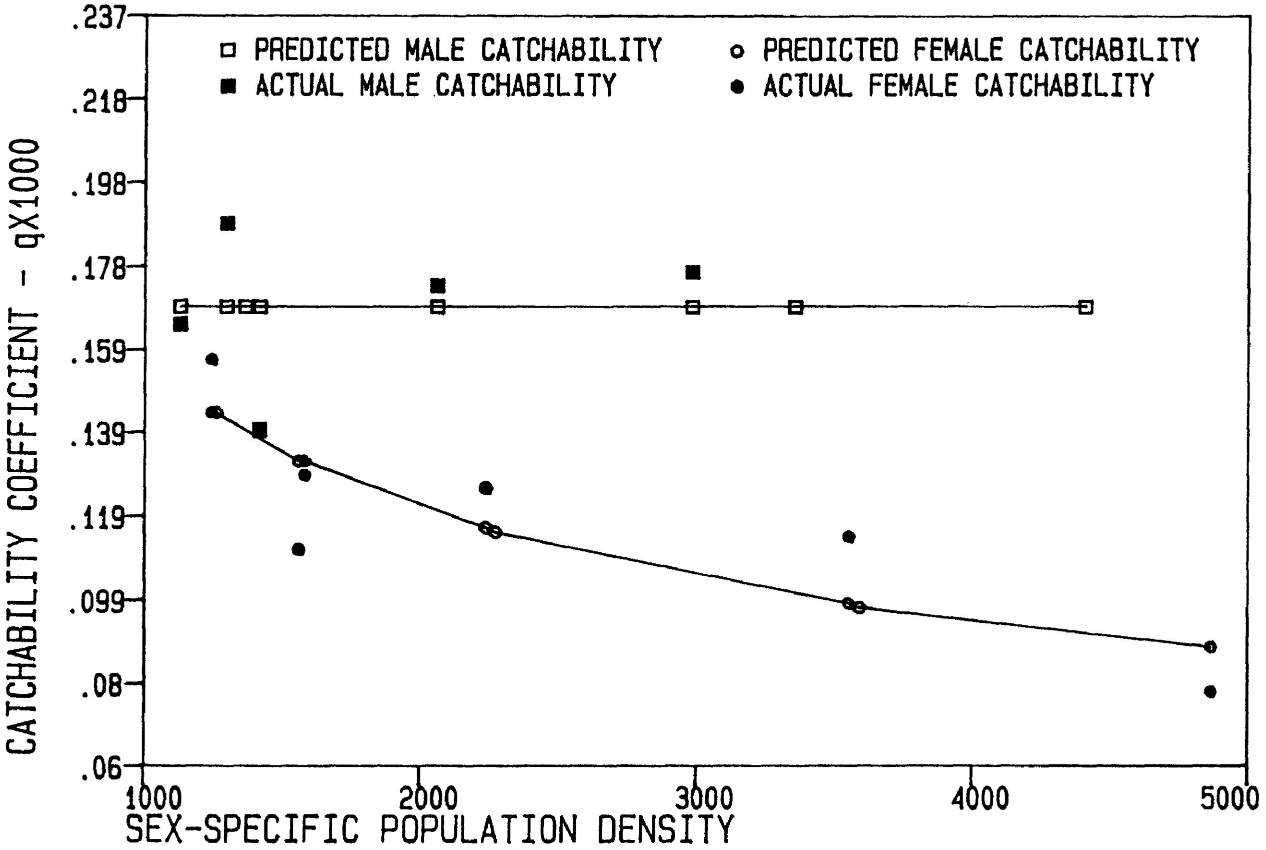
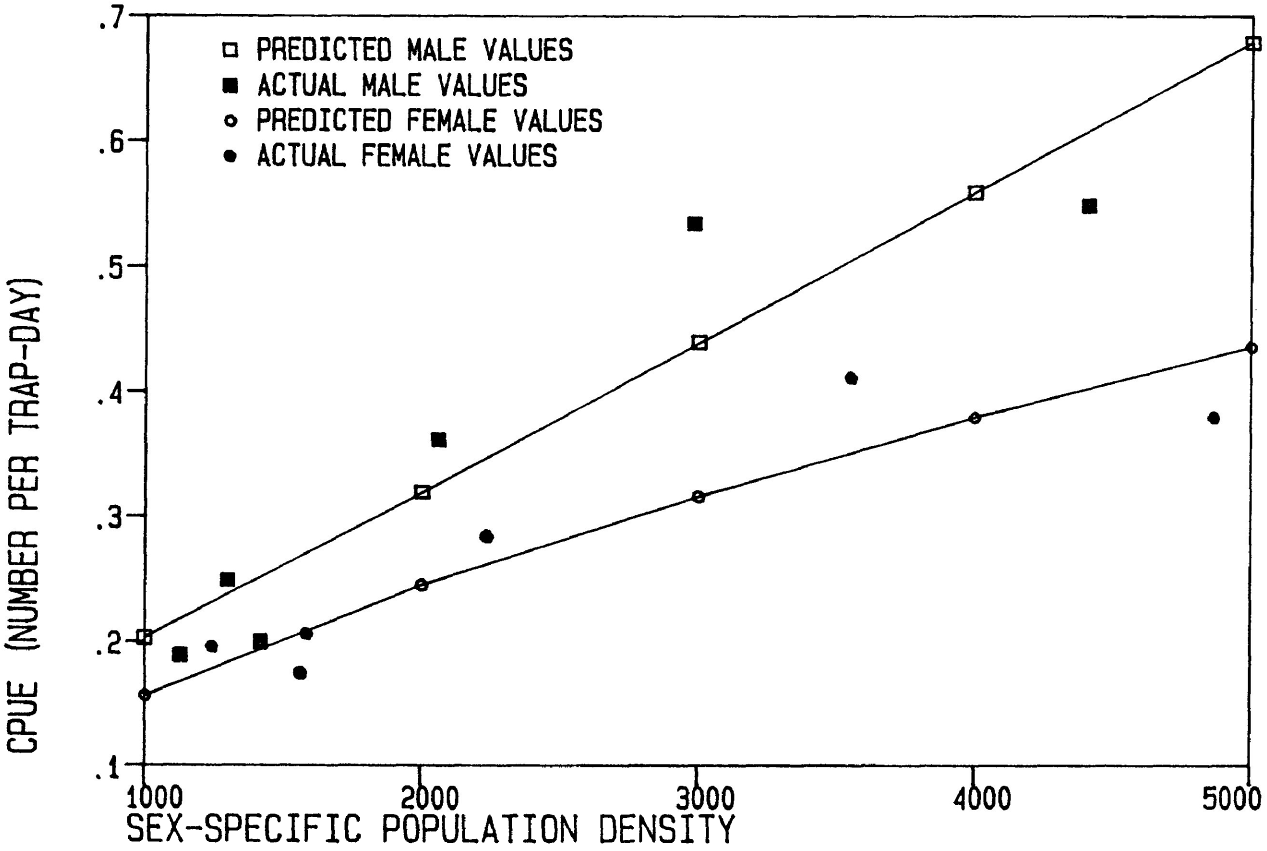

□ PREDICTED MALE CATCHABILITY
■ ACTUAL MALE CATCHABILITY
○ PREDICTED FEMALE CATCHABILITY
● ACTUAL FEMALE CATCHABILITY
CATCHABILITY COEFFICIENT - qX1000
.237
.218
.198
.178
.159
.139
.119
.099
.08
.06
1000
2000
3000
4000
5000
SEX-SPECIFIC POPULATION DENSITY

Figure 5. Relationships between male and female catch-per-unit-effort (CPUE) and abundance in Dock Lake 1977-1985. Regression line, male: $Y=0.000119X+0.08226$, $R2=0.87$ ($P<0.006$), for relationship between CPUE (Y) and absolute male density (X). Regression line, female: $\ln Y=0.6336 \ln X-6.227$, $R2=0.87$ ($P<0.005$), for relationship between logarithmically transformed (Napierian logarithm) CPUE (Y) and logarithmically transformed absolute density (X).



□ PREDICTED MALE VALUES
■ ACTUAL MALE VALUES
○ PREDICTED FEMALE VALUES
● ACTUAL FEMALE VALUES
CPUE (NUMBER PER TRAP-DAY)
.7
.6
.5
.4
.3
.2
.1
1000
2000
3000
4000
5000
SEX-SPECIFIC POPULATION DENSITY

trap-days female catchability varied inversely. At 6000 trap-days male catchability decreased. Since variation in q was related to interactions between CPUE and sampling intensity, 1977, 1978 and 1984 data were therefore excluded from further catchability analysis. Increasing density did not effect males but female catchability decreased (Fig. 4). Females therefore experienced significantly higher fishing mortality per unit of effort at lower densities (i.e., catchability was density-dependent).

This density-dependent catchability invalidates the assumption of a proportional relationship between female CPUE and abundance. Male abundance accounted for 87% of the variation in CPUE up to 4000 trap-days effort (Fig. 5). The relationship between female abundance and CPUE was significantly curvilinear ($P<0.005$) explaining 87% of the variability (Fig. 5).

The nonlinear relationship between female catchability and abundance could be either the result of gear saturation or a functional response (Rothschild 1977; Peterman and Steer 1981). Sampling intensity was constant from 1979 to 1985, however changes in CPUE (Fig. 1 and 2) and relative catch composition (Table 4) indicates a temporally changing functional response. The relationship between percent harvest and fishing effort up to 4000 trap-days was linear ($P<0.0003$) for males (Fig. 6). However the harvest rate-fishing effort relationship for females was nonlinear ($P<0.0001$) indicating a functional response (Fig. 6). As harvest duration increased (without changing the number of traps) female vulnerability decreased.

At 6000 trap-days effort catchability decreased for both males and females, even though the percent harvested remained

Figure 6. Relationships between sex-specific percent harvest and nominal effort in Dock Lake 1977-1985. Regression line, male: $Y=0.0001094X+0.1726$, $R2=0.83$ ($P<0.0003$), for relationship between percent harvest (Y) and nominal effort (X). Regression line, female: $\ln Y=0.6197 \ln X-5.984$, $R2=0.92$ ($P<0.0001$), for relationship between logarithmically transformed (Napierian logarithm) percent harvest (Y) and logarithmically transformed nominal effort (X).

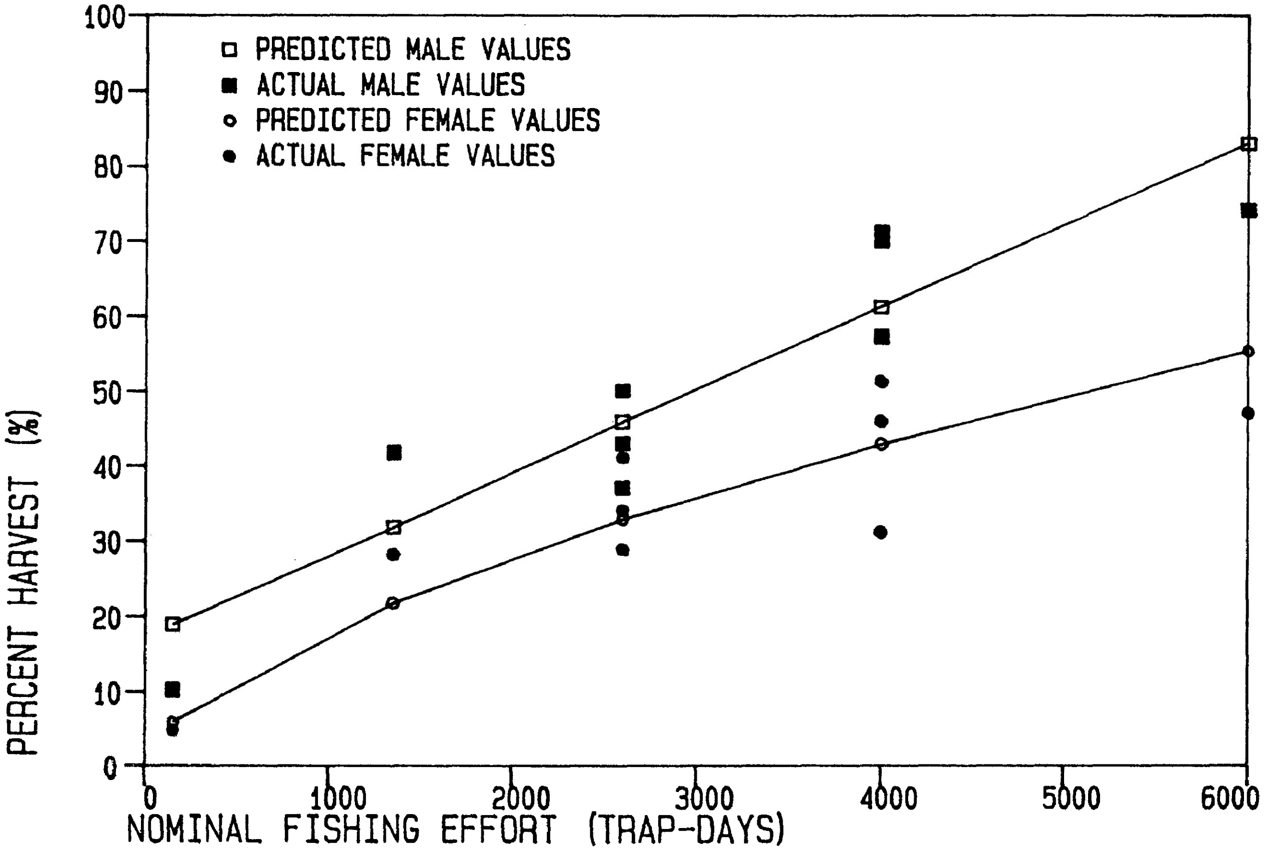

□ PREDICTED MALE VALUES
■ ACTUAL MALE VALUES
○ PREDICTED FEMALE VALUES
● ACTUAL FEMALE VALUES
PERCENT HARVEST (%)
0
10
20
30
40
50
60
70
80
90
100
0
1000
2000
3000
4000
5000
6000
NOMINAL FISHING EFFORT (TRAP-DAYS)

Figure 7. Male exploitation rates (u) 1977-85 based on mark-recapture, harvest-population density and catchability estimates.

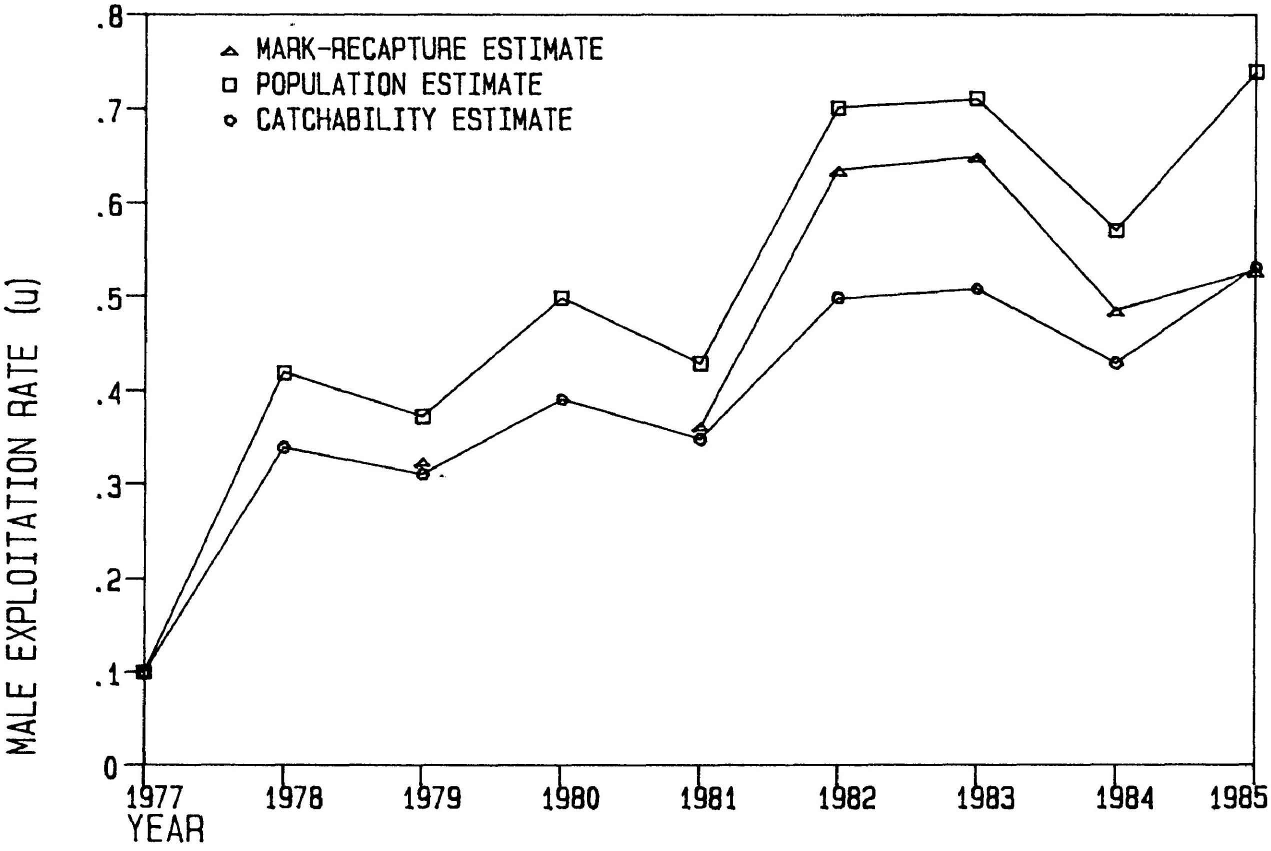
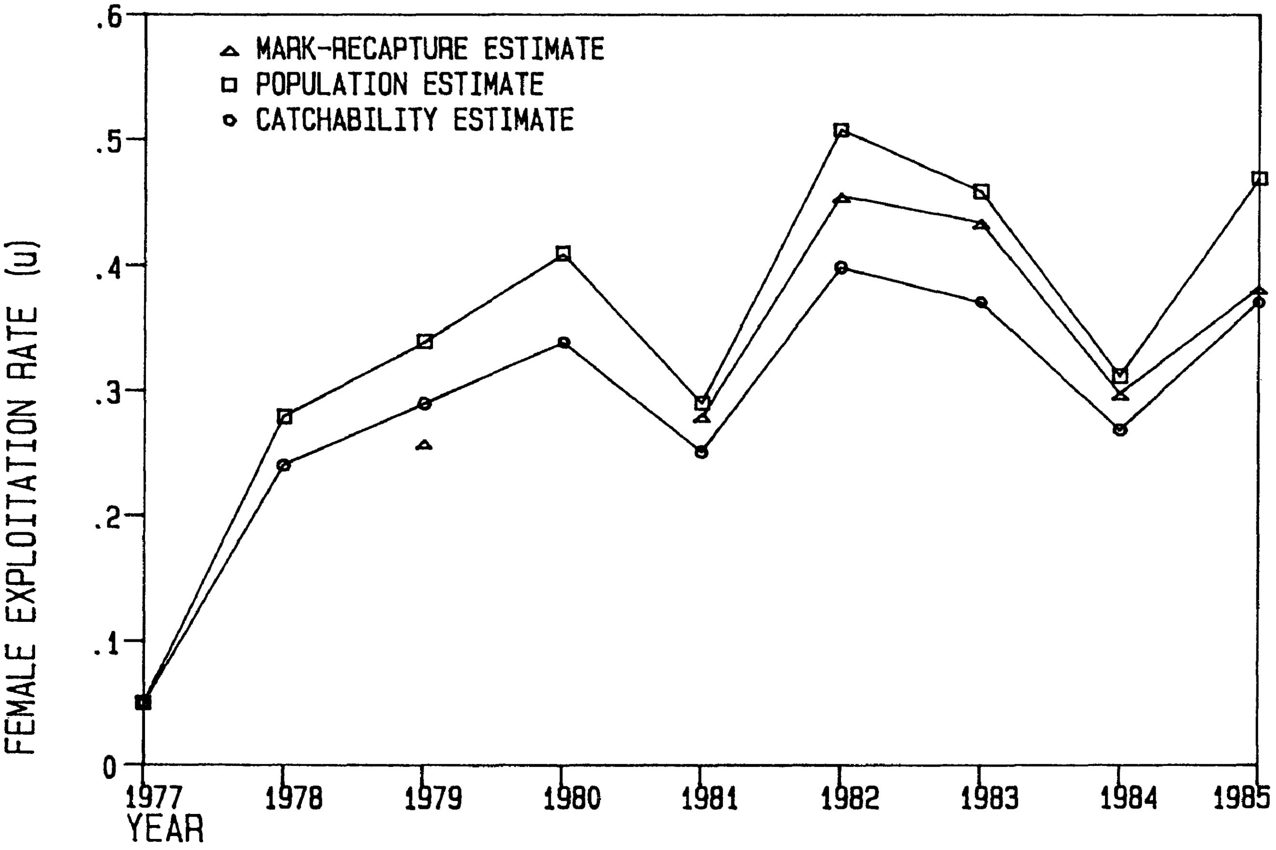

△ MARK-RECAPTURE ESTIMATE
□ POPULATION ESTIMATE
○ CATCHABILITY ESTIMATE
MALE EXPLOITATION RATE (u)
.8
.7
.6
.5
.4
.3
.2
.1
0
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

Figure 8. Female exploitation rates (u) 1977-85 based on mark-recapture, harvest-population density and catchability estimates.


△ MARK-RECAPTURE ESTIMATE
□ POPULATION ESTIMATE
○ CATCHABILITY ESTIMATE
FEMALE EXPLOITATION RATE (u)
0
.1
.2
.3
.4
.5
.6
1977
1978
1979
1980
1981
1982
1983
1984
1985
YEAR

constant when compared to 4000 trap-days of effort (Fig. 4 and 6). Apparently employing the same sampling intensity (i.e., 200 traps) led to time saturation between harvests. We could not harvest more than 60% of the exploitable stock irregardless of sampling intensity or duration.

Exploitation Rates

The mark-recapture technique, used for determining population density prior to the harvest, provided the opportunity to assess the precision and bias in estimating exploitation rates. The number of marked recaptured crayfish in the harvest relative to the total number of marked individuals in the population provide an unbiased exploitation rate estimate (Ricker 1975, page 77). This assumes that marked and unmarked individuals randomly mix. The 1979 and 1981-85 harvests have complete records of marked crayfish caught. The proportion of the exploitable stock caught each year provided another possible estimate of exploitation rate (Ricker 1975, page 163). Exploitation rates were also calculated from catchability and nominal fishing effort (Ricker 1975, page 178).

Exploitation rate estimates derived from the proportion of the exploitable stock harvested proved to be consistently higher than those derived from recapture rates or catchability (Fig. 7 and 8). This between-estimate disparity increased at efforts of 4000 trap-days and greater, especially for males. Female exploitation rate estimates varied only 10%. At 6000 trap-days effort the `unbiased' mark-recapture estimate equaled the catchability estimate, while the proportional harvest estimate was significantly higher. Throughout this period the number of sampling units had remained constant (200 traps) while the duration of harvest increased. Since increases in sampling duration decreases the relative proportion of age II males in the catch this alters age- and sex-specific trapabilities (Table 4). Apparently smaller crayfish were discouraged by these males from entering the traps during the harvest, and logically during the preceding population estimate (when the crayfish were marked). This effect is apparent from the harvest data where the mean size of marked male and female crayfish is larger ($P<0.001$) than the unmarked crayfish in all years (Table 1). Consequently as the daily proportion of harvested small crayfish increased, this dilution of the ratio of marked to unmarked individuals increased as sampling duration increased. The result was an underestimation of exploitation rates at higher efforts.

DISCUSSION

An increase in nominal effort changed the catchability of the sexes and various age groups. Catchability was determined by the three interacting factors: sampling intensity, sampling duration and behavioural response. As sampling intensity increased expected total CPUE (compared to total annual harvest) decreased (Fig. 1 and 2). At 250 traps gear competition lowered CPUE and reduced yield. Use of 200 traps produces a subtle effect on harvest as sampling duration increases. Although yield increased with increases in nominal effort, expected CPUE's actually declined. At 4000 trap-days, daily catch and CPUE were directly proportional to the number of days but lower efforts (2600 trap-days) produced higher CPUE's, while higher efforts (6000 trap-days) produced lower than expected CPUE's (Fig. 1 and 2). Vulnerability of age II male crayfish as modified by changes in sampling intensity and sampling duration appears responsible for this phenomenon. The daily catch of large males in Dock Lake was inversely related to sampling effort. Abrahamsson (1966) also observed large males dominating the early catches of **Astacus astacus** Linne at intensive fishing efforts. Most fisheries managers assume a linear relationship between CPUE and stock abundance. However, the variation in Dock Lake age- and sex-specific catchability emphasizes the importance of verifying this underlying assumption.

A number of studies (Capelli 1975; Capelli and Magnuson 1983; France 1985; Lodge, Kratz and Capelli 1986) have estimated relative abundance of crayfish by using male CPUE caught in modified minnow traps as an index of abundance. However in Dock Lake, male CPUE was inversely related to sampling intensity. Thus use of CPUE would have significantly over-estimated abundance, unless corrected for trap spacing (i.e., sampling intensity). The variable catchability of Marron **Cherax tenuimanus** (Smith) is influenced in a similar manner (Morrissy 1975). CPUE should therefore be expressed in terms of the area sampled so as to provide comparable relative estimates of population density (Morrissy 1975). A suggestion for crustacean fishery assessment is that sampling design should standardize the effort per unit of area as opposed to sampling with constant effort.

The precision of CPUE abundance estimates is directly related to trap spacing (per unit length of shoreline and per unit area of littoral zone). When linear spacing was approximately the same as the "effective diameter of noncompetitive gear density" (Morrissy 1975), changes in population density were paralelled by similar changes in Dock Lake male CPUE. For our crayfish population, sampling with between-trap spacing of 3 m, positioned parallel to the shoreline at depths of <1.5 m, was proportional to the estimated noncompetitive gear diameter of 6.3 m (i.e., 200 traps for 6292 m^2 of littoral zone habitat). Thus standardizing the sampling area ratio (i.e., sampling unit per length of shoreline to the effective gear diameter based on available habitat in the littoral zone) should provide accurate CPUE indices of abundance and may be a suitable technique for assessing other benthic crustaceans.

The nonlinearity between female catchability q and population density is a functional response (Holling 1959). Such a response can be considered as a depensatory mortality factor (Peterman 1977; Crecco and Savoy 1985). Furthermore it significantly reduces the accuracy of CPUE data as a predictor of female abundance. Management of a stock that becomes more vulnerable at low densities severely challenges fisheries managers. In such cases the inherent danger of female recruitment overfishing becomes disguised by high male CPUE and large average size of males.

Furthermore we found that exploitation helped stabilize the age structure of the exploited population. This is because younger age classes were harvested in proportion to their abundance (Table 4). However males were more vulnerable than females to exploitation. While the percent male harvest increased commensurate with nominal effort until 4000 trap-days, the proportion of females harvested declined (Fig. 6). For example while the 1985 harvest at 6000 trap-days effort removed 74% of the exploitable male stock it only caught 47% of the female stock. At this level of effort both male and female populations were stressed. The most obvious indicator was the decline in the CPUE-total harvest ratio (Fig. 1 and 2). The small average size and the large percentage of crayfish <30 mm are suggestive of recruitment overfishing which could lead to stock collapse. Potential overharvest could be predicted through employing the following indicators: CPUE-total harvest ratio, the percent harvest-fishing effort relationship and the CPUE-abundance relationship. Assessment of a crayfish stock could be performed prior to the harvest. Potential yield could be forecasted from a standardized male CPUE sample (Fig. 6). Such short-term forecasting would facilitate management of the fishery. This would produce a flexible management strategy based on effort regulation. Assessment of crayfish stocks using our indices are preferable to traditional methods which suffer from cost constraints and limited available time. Ideally the fishery itself would provide the information necessary to assess the status of the population based on the harvest trends.

Estimated exploitation rates that were based on mark-recapture methods were imprecise and biased at high nominal efforts. The changing trapability of smaller crayfish was related to behavioural trap dominance of age II males. The increased relative abundance of small crayfish significantly altered the proportion of marked crayfish in the daily catch. The detection of overharvest using exploitation rates based on recaptured marked individuals would be difficult at high nominal efforts. At 6000 trap-days effort, using mark-recapture ratios, we underestimated the male exploitation rate by 40%. The female recapture ratio underestimated the exploitation rate by 27%. The increase in nominal effort to 6000 trap-days resulted in increased total annual yield. However deviation in age- and sex-specifc exploitation relationships and time saturation confounded possible indices of overharvest. Detection of overfishing using mark-recapture techniques would be impossible for crayfish stocks exploited at high levels of nominal effort.

We feel the assessment and management of wild crayfish stocks based on our indices are both practical and economical. Our long-term study suggests potential overharvest to be unlikely at exploitation levels dictated by economic feasibility. Dock Lake crayfish sustained constant yields of 25-35 kg (i.e., 40-55 $kg.ha^{-1}$ of littoral zone <1.5 m depth) at 4000 trap-days effort (200 traps for 20 days). Increasing the nominal effort to 6000 trap-days did not increase CPUE or exploitation rates of Dock Lake males or females (Fig. 1 and 2). The maximum harvest that can be obtained with this passive fishing gear was fixed at 75% of the males, 50% of the females or 60% of the exploitable stock regardless of fishing intensity or fishing duration. Changing catchability between 4000 and 6000 trap-days effort produced similar exploitation rates. Obviously the underlying assumptions that fishing effort is proportionately related to mortality needs testing. However at high harvest levels (6000 trap-days) the increased proportion of sexually immature individuals in the catch is suggestive of over-fishing (Table 2). However decreasing vulnerability to severe fishing effort provides some protection, mostly from extirpation, rather than over-exploitation. Northern crayfish stocks can sustain annual exploitation rates over 50%. This exploitation level can be attained using predetermined nominal efforts since harvest fluctuates with exploitable stock density. To achieve this harvest would require a large number of minnow traps fished for a long time (i.e., similar to 4000 trap-days effort). At this effort harvesting with passive gear, such as modified minnow traps, becomes tremendously inefficient and uneconomical given the yields obtained. Management becomes by necessity directly related to trapability. The development of active capture gear while significantly improving the feasibility of economically harvesting wild stocks of crayfish in northern Ontario might change the susceptibility of stocks to overharvest. Use of active gear would therefore have to be re-evaluated.

Authors' Note. Dock Lake's exploitable population decreased 45% from 9273 in 1985 (4410 males and 4863 females) to 5109 in 1986 (2302 males and 2807 females). The 1986 harvest of 6000 trap-days effort removed 75% of the males (1733) and 46% of the females (1286); the annual exploitation rate was 59% (3019 of 5109). Apparently these high levels of effort over-exploited the crayfish population without altering the percentage harvested. Catchability remained unchanged (male $q = 0.1233 \times 10^{-4}$; female $q = 0.0764 \times 10^{-4}$) from 1985.

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POPULATION REGULATION

"So, we complicate our models step by step, hoping that before we pass into the abyss of mathematical intractability, a reasonable compromise will have been struck between precision and generality."

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ABSTRACT

Changes in growth/mortality rates during the male age I-to-age II life stage strongly regulate year-class strength, annual growth and, ultimately reproduction and population growth potential of northern crayfish populations of **Orconectes virilis**. During the age I-to-age II life stage males reaching sexual maturity become behaviourally dominant over smaller conspecifics and females. This advantage manifests itself in increased individual male breeding success. These males regulate growth/mortality rates of the juvenile life stages (i.e., egg-to-young-of-year (YOY) and YOY-to-age I) in the population. In the control population of Shallow Lake juvenile life stages exhibit strong density-dependent regulation. This results in a dynamic and oscillatory inverse relationship between age I-to-age II male growth and female year-class strength which then correlates with cohort egg production. Exploitation breaks down these dynamic processes so that in Dock Lake, male and female year-class strength correlates with annual growth, while cohort egg production varies independently. These responses allow the crayfish population to increase regardless of fishing pressure. Paradoxically, this increased population growth/yield is dependent upon annual removal of 70% of the age I males. Our results suggest that populations destabilize and become oscillatory with implementation of size or sex limitations. Thus the worst management scenario involves a male only fishery with a size limit set above the onset of sexual maturity. Restrictive harvest tactics for crayfish and possibly other benthic crustaceans should be re-evaluated.

INTRODUCTION

Direct quantitative assessments of population vigour related to biological and environmental variation provide useful management indices. However use of a single descriptive statistic to quantify demographic vigour reveals nothing about the resilience of a population to sudden environmental perturbations (Hanks 1981). The successful prediction of population responses and potential yields depends upon the availability of long-term, accurate data and demonstrated relationships between various life history stages (Phillips 1986). However empirical tests of hypothesized population relationships are rarely encountered (in the literature). For these reasons we monitored populations of the crayfish, **Orconectes virilis** (Hagen), in northwestern Ontario subjected to both natural environmental variation and varying degrees of human exploitation over the past decade. This time trend series permits analysis of: biological processes, environmental forces, human activities and their interactions. The outcome of these 'naturally' occurring events produces variation in growth, mortality and reproduction which in turn regulates population density.

Responses to random variation and induced perturbation are reflected as differences in mortality and growth patterns of various life stages between the exploited (Dock Lake) and control population (Shallow Lake). Long-term changes in population parameters indicate crayfish self-regulate. We believe exploitation suppresses the biotic negative feedback mechanism controlling both young-of-year (YOY) recruitment and juvenile survival (YOY-to-age I). Both stages critically influence ultimate year-class strength, levels of reproduction and growth of the population.

We believe the dominance hierarchy of crayfish to be responsible for this feedback mechanism. Dominance is directly related to size with sexually mature males dominating both males and females (Bovbjerg 1956). We believe this behaviour regulates mortality and growth of various life stages as well as reproductive potential of these crayfish populations. Variation in these life stage-specific interactions dramatically effects population dynamics.

Despite the apparent evolutionary advantage for maintenance of a well regulated population, the proximal advantage for male crayfish is improved individual fitness. Individual fitness is defined as the average reproductive success, i.e., an animal increases its fitness if it increases its genetic contribution to future offspring (Orians 1969). At 32.8 mm carapace length (standard deviation = 2.66) male crayfish become sexually mature. Size frequency analysis reveals this to be the approximate boundary of overlap between age I and age II. Therefore the size-dependent competitive ability of maturing adult (age I-to-age II) male crayfish regulates population growth principally through changes in their growth and mortality rates .

Since exploitation principally effects the mortality of age I-to-age II crayfish, we examined the effect of increased harvest on age- and sex-specific growth and mortality rates. Comparisons between control and exploited populations helped separate intrinsic from extrinsic regulating factors. From these conceptual insights we developed a deterministic model of crayfish population dynamics based on comprehensive life history features useful for the development of management options. Our approach integrates the qualitative aspects of life history phenomena with the quantitative analysis of life stage growth/mortality inter-relationships.

STUDY AREA AND METHODS

The study area's physical and chemical properties as well as general sampling methods have been described elsewhere (Momot 1978; Morgan 1987); only additional methods pertinent to this portion of the study are described here. Since 1977 crayfish in Dock Lake have been harvested with modified minnow traps. Originally we sought to over-exploit the population in Dock Lake while having the nearby unexploited population in Shallow Lake serve as a control. This control-treatment empirical study allowed for the testing of population regulation hypotheses.

The harvest of Dock Lake's crayfish population began in 1977 with an initial nominal effort of 150 trap-days (30 traps for 5 days). A trap-day is one minnow trap fished 24 hours. In 1978 the effort was increased to 1350 trap-days (150 traps for 9 days). From 1979 to 1981, effort was raised to 2600 trap-days (200 traps for 13 days). In 1982 the effort was further increased to 4000 trap-days (200 traps for 20 days). This nominal effort was maintained for 1983 and 1984. However in 1984 the fishing intensity changed to 250 traps without a corresponding change in fishing effort (250 traps for 16 days). Since the crayfish population did not exhibit any signs of over-exploitation we increased the effort in 1985 to the present level of 6000 trap-days (200 traps for 30 days). Harvest began in late July and was completed by the end of August. Crayfish age I and older were susceptible to the gear.

Our experimental design approximates the Type I fishery of Ricker (1975, page 10) in that population estimates precede the harvest. Therefore the biological year (i.e., for estimating mortality and growth rates) starts at the time fishing begins, with natural mortality occurring after fishing ends. Thus total annual mortality is easily separated into discrete time steps made up of fishing and natural components.

We examined the variability in vital parameters (growth, mortality and annual recruitment patterns) and attempted to explain the underlying causes and mechanisms for population change. We began by running a series of regression trials to test the possible density dependence of age- and sex-specific mortality and growth rates. Additional regression analysis tested the relationships between growth and mortality rates both within life stages and by sex.

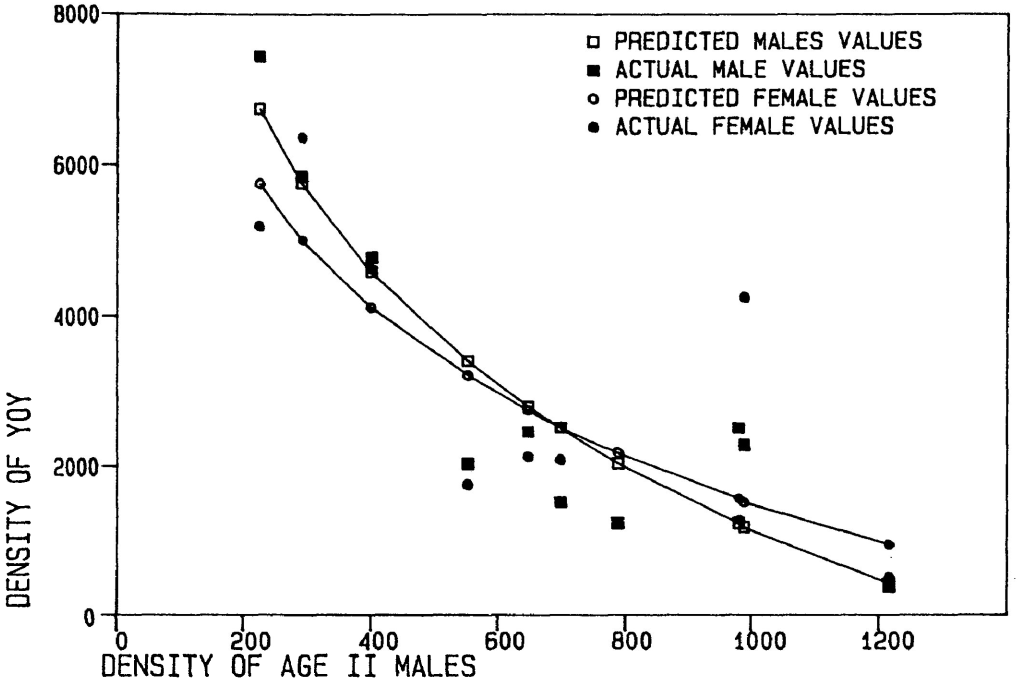
The effect of random variation (in population parameters) caused by environmental processes/forcing on population dynamics was evaluated using linear and step-wise multiple regression techniques. Variability in population parameters caused by environmental processes was evaluated using linear regression (i.e., determine correlation between life stage density, growth and mortality, and climatic variables). Evaluation of population dynamics influenced by both density-dependent relationships and environmental forcing was analysed using multiple regression. Intensity and frequency of heat input and precipitation was calculated from yearly meteorological records obtained from the nearby Thunder Bay Airport (48° 22' N 89° 19' W). We hoped to separate the effect of the environmental component from the detailed interactions between life stages.

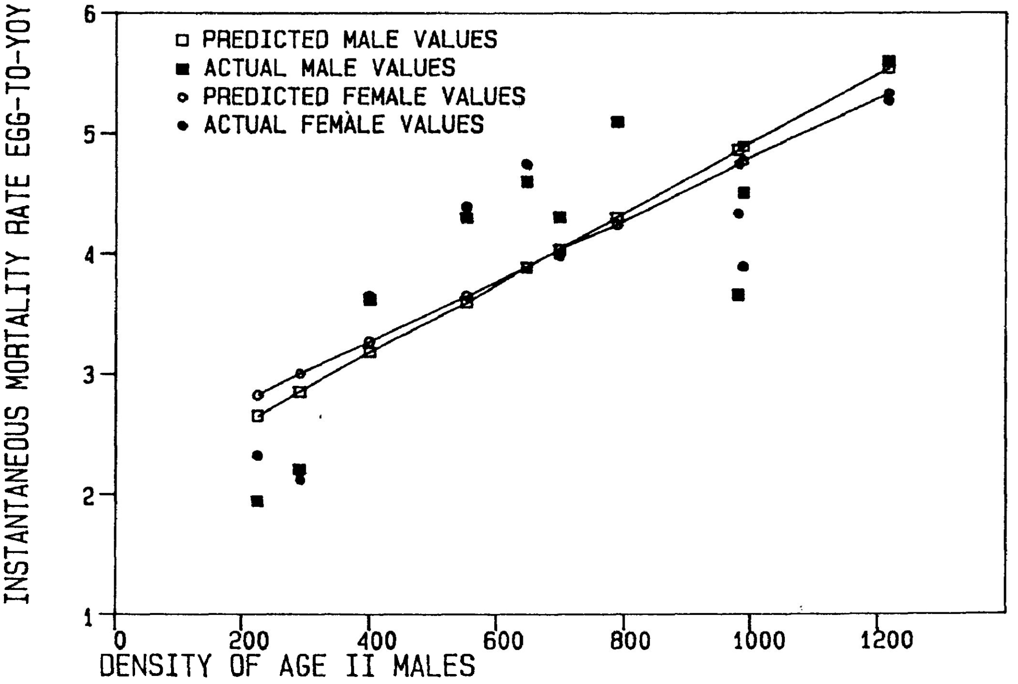
Indices of relative year-class strength and relative growth were calculated for males and females using the method described by Mann (1973, 1976). An index of relative egg production was derived by comparing the percentage of a particular year-classes egg output with the average egg output for females of that age over the entire decade of the study. These were summed over the entire cohort life span to calculate mean indices. These methods were used for both between-sex as well as between-lake comparisons of yearly variability in the exploitable stock.

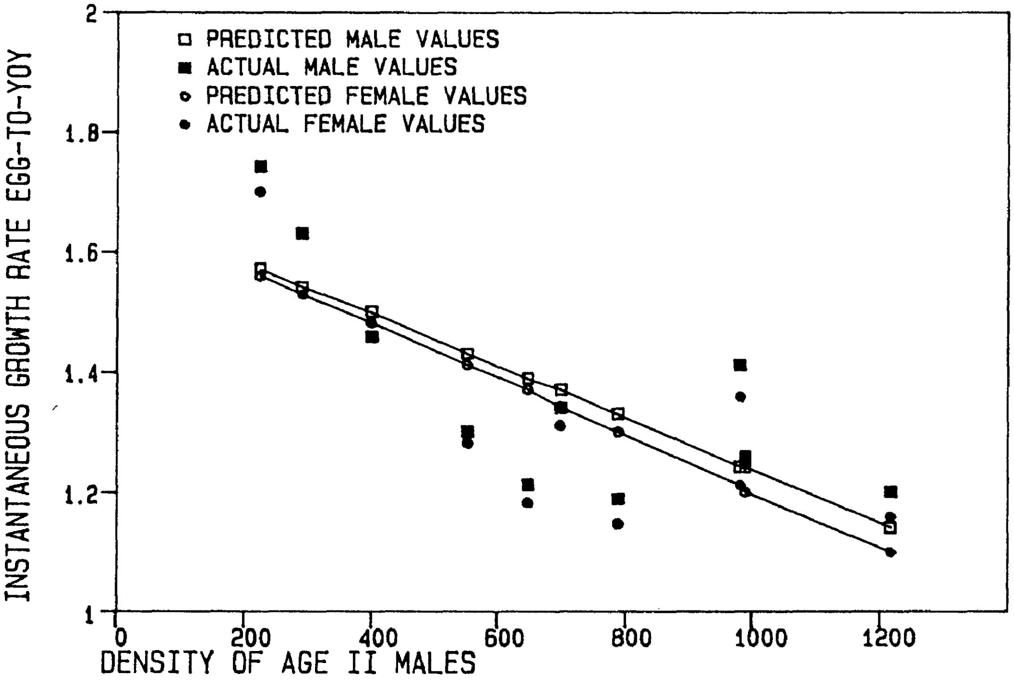
In this paper, we define crayfish life stages which will be used to separate age classes. These descriptive terms also designate reproductive condition in males and females. The life cycle is characterized by three stages: (1) hatchling - **egg-to-young-of-year** (YOY), this is the period from spring (when the eggs are extruded) to the end of the first growing season; (2) juvenile - **YOY-to-age I**, during this stage females attain sexual maturity and recruitment to the exploitable stock is determined; and (3) adult - **age I-to-age II**, this is the life stage when males mature and are capable of moulting into the sexualy active form I condition.

Figure 1. Relationships between male age II density and young-of-year (YOY) density and hatching-to-YOY growth and mortality rates in Dock and Shallow Lake. Shallow Lake regression lines, $Y=-3735\ln X+2.6940$, $R2=0.85$ $(P<0.0001)$, and $Y=-2838\ln X+21090$, $R2=0.62$ $(P<0.004)$, for relationship between density of young-of-year (Y) and logarithmically transformed (Napierian logarithm) density of age II males (X), for male and female young-of-year, respectively; $Y=0.002892X+2.011$, $R2=0.65$ $(P<0.002)$, and $Y=0.002534X+2.251$, $R2=0.60$ $(P<0.004)$, for relationship between instantaneous mortality rate from egg-to-YOY (Y) and density of age II males (X), for male and female crayfish, respectively; $Y=-0.0004402X+1.673$, $R2=0.57$ $(P<0.006)$, and $Y=-0.0004707X+1.670$, $R2=0.61$ $(P<0.004)$, for relationship between instantaneous growth rate from egg-to-YOY (Y) and density of age II males (X), for male and female crayfish, respectively. Dock Lake regression lines, $Y=0.001666X+2.594$, $R2=0.94$ $(P<0.0003)$, and $Y=0.002328X+2.181$, $R2=0.82$ $(P<0.004)$, for relationship between instantaneous mortality rate from egg-to-YOY (Y) and density of age II males (X), for male and female crayfish, respectively.

SHALLOW LAKE

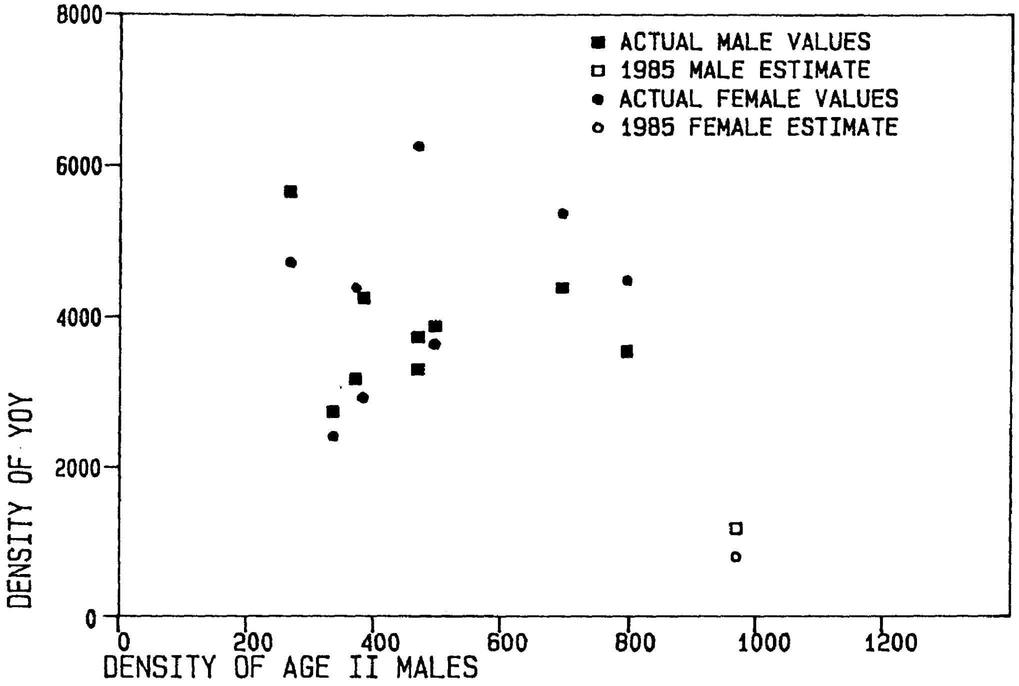


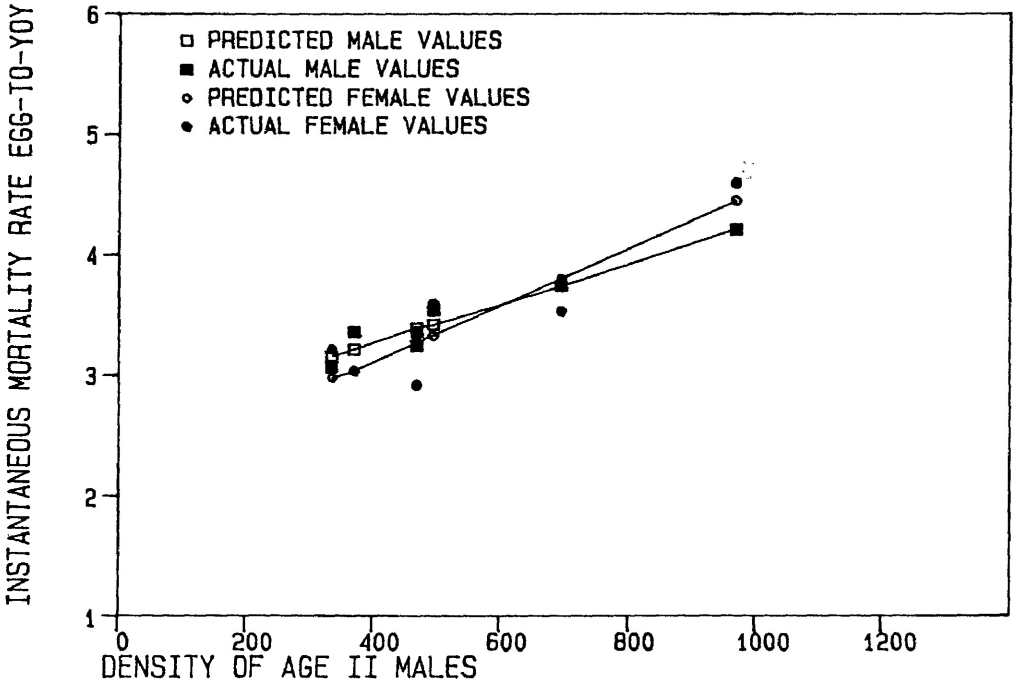


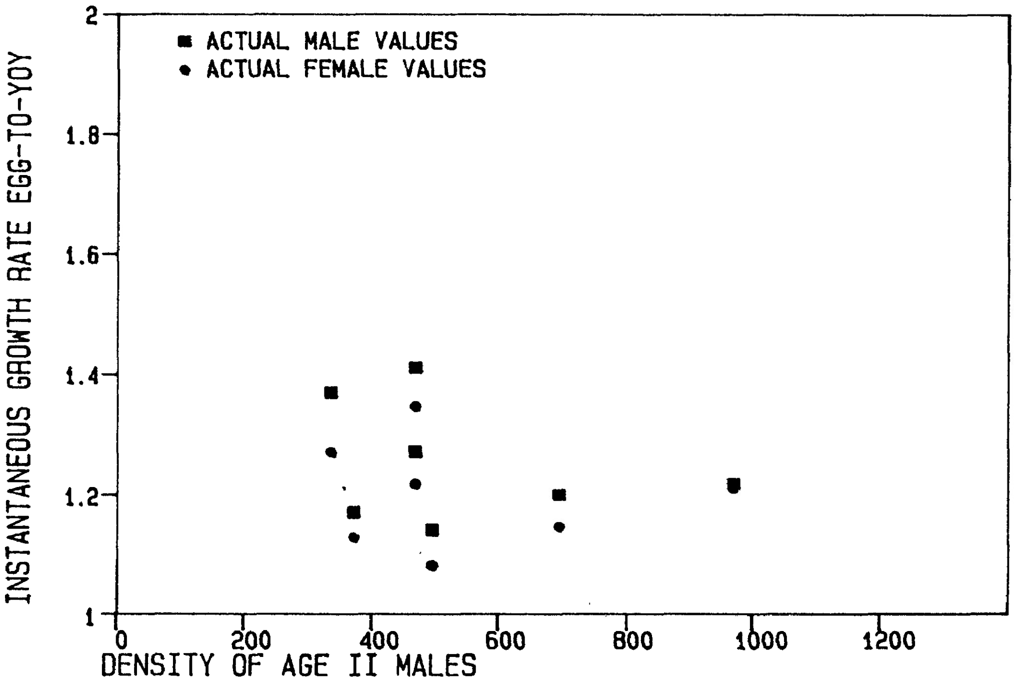


PREDICTED MALE VALUES
ACTUAL MALE VALUES
PREDICTED FEMALE VALUES
ACTUAL FEMALE VALUES
INSTANTANEOUS GROWTH RATE EGG-TO-YOY
DENSITY OF AGE II MALES
2
1.8
1.6
1.4
1.2
1
0
200
400
600
800
1000
1200

DOCK LAKE


■ ACTUAL MALE VALUES
□ 1985 MALE ESTIMATE
● ACTUAL FEMALE VALUES
○ 1985 FEMALE ESTIMATE
DENSITY OF YOY
8000
6000
4000
2000
0
0
200
400
600
800
1000
1200
DENSITY OF AGE II MALES


□ PREDICTED MALE VALUES
■ ACTUAL MALE VALUES
○ PREDICTED FEMALE VALUES
● ACTUAL FEMALE VALUES
INSTANTANEOUS MORTALITY RATE EGG-TO-YOY
6
5
4
3
2
1
0
200
400
600
800
1000
1200
DENSITY OF AGE II MALES



■ ACTUAL MALE VALUES
● ACTUAL FEMALE VALUES
INSTANTANEOUS GROWTH RATE EGG-TO-YOY
2
1.8
1.6
1.4
1.2
1
0
200
400
600
800
1000
1200
DENSITY OF AGE II MALES

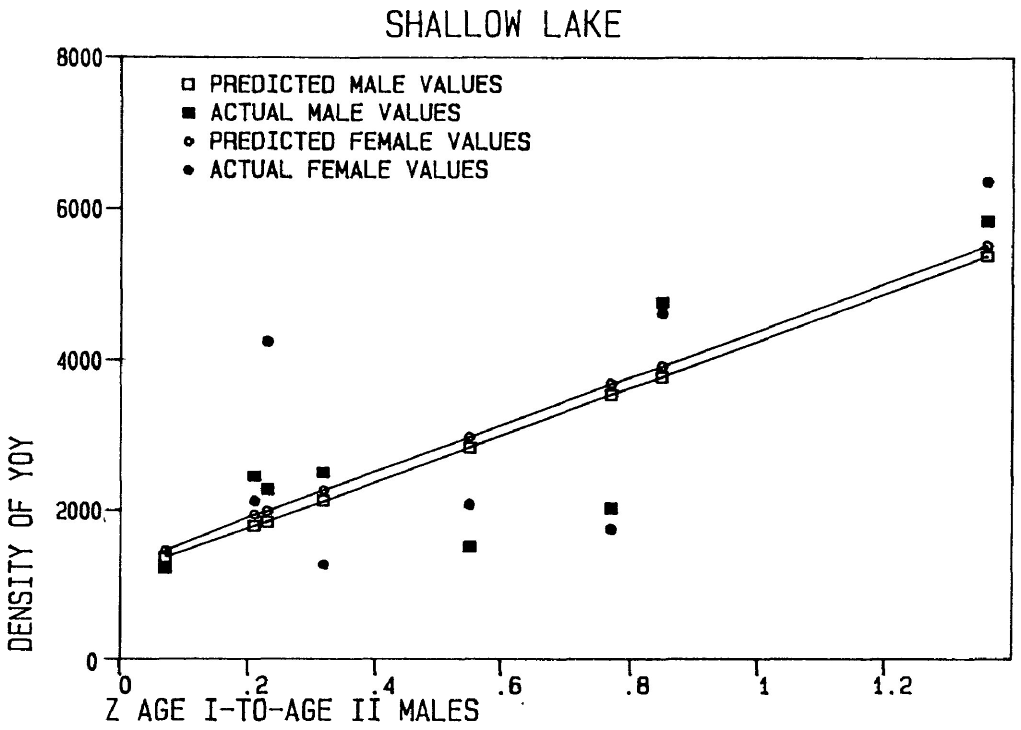
RESULTS

We investigated the possible effect of environmental variation in determining population density or life history parameters by using least-squares linear regression analysis together with step-wise multiple regression (Zar 1974). Weather parameters were arbitrarily defined from climatological data. We expected that variance in environmental conditions (i.e., temperature and precipitation) would strongly affect life history parameters through its influence on metabolic rates and thresholds. Age- and sex-specific growth rates, mortality rates and density are independent of year-to-year variation in energy inputs and precipitation (i.e., mean temperature, coefficient of variation, growing-degree-days above 10°C and 15°C, and amount of rainfall) during the growing season (Morgan 1987). Also no consistent pattern of a relationship between environmental variation and deviations in relative rates has emerged. Environmental forcing failed to influence the life history parameters affecting population dynamics in Dock or Shallow Lake crayfish. There appears to be no evidence of passive environmental factors regulating these populations (Morgan 1987).

Changes in yearling-to-adult mortality patterns in Shallow Lake appears to influence growth and mortality relationships of egg-to-YOY and YOY-to-age I age groups. Variation in recruitment is the result of adjustments in growth/mortality rates between the egg and juvenile life stages (i.e., prereproductive sizes/ages). In Shallow Lake, YOY recruitment is solely dependent upon the density of sexually mature age II males (Fig. 1).

Further regression analysis reveals the influence of male

Figure 2. Relationships between male age I-to-age II total instantaneous mortality (Z) and male and female YOY density in Dock and Shallow Lake. Shallow Lake regression lines, $Y=3093X+1137$, $R2=0.67$ ($P<0.008$), and $Y=3141X+1247$, $R2=0.52$ ($P<0.04$), for relationship between density of young-of-year (time t+1) (Y) and male instantaneous mortality rate from age I-to-age II (t) (X), for male and female young-of-year, respectively.


SHALLOW LAKE

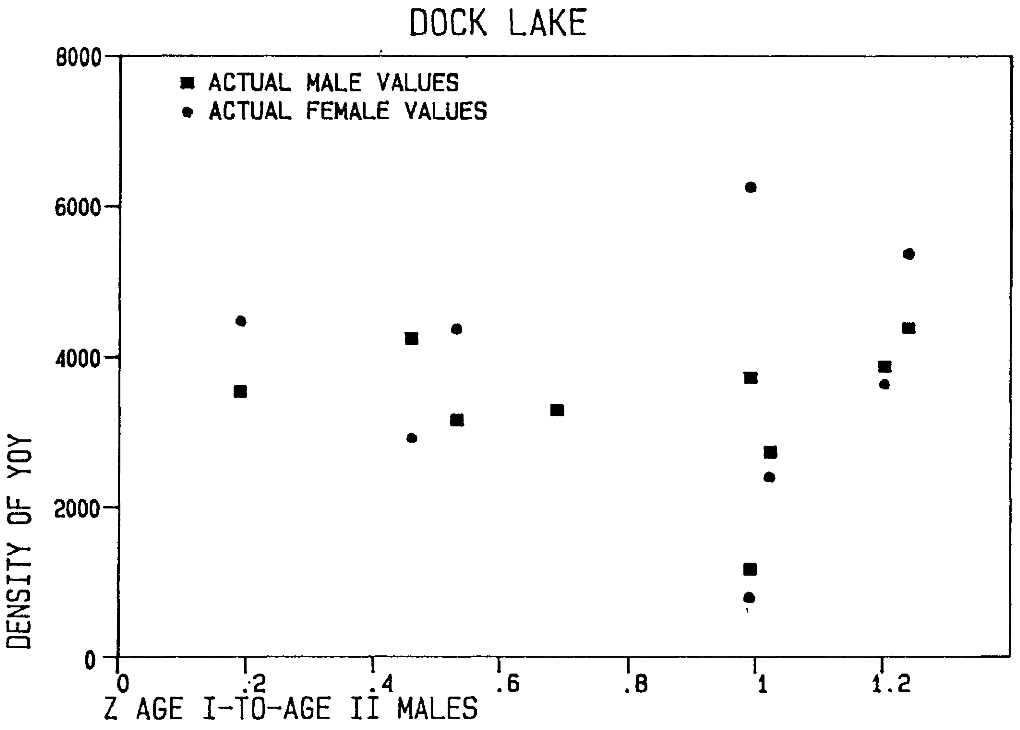
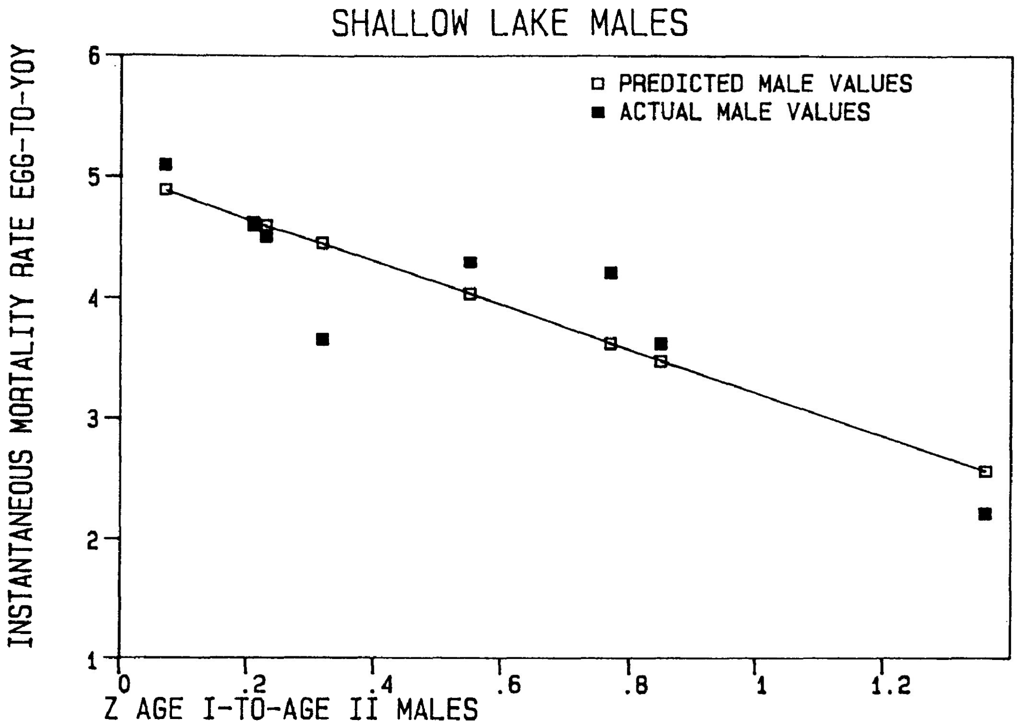
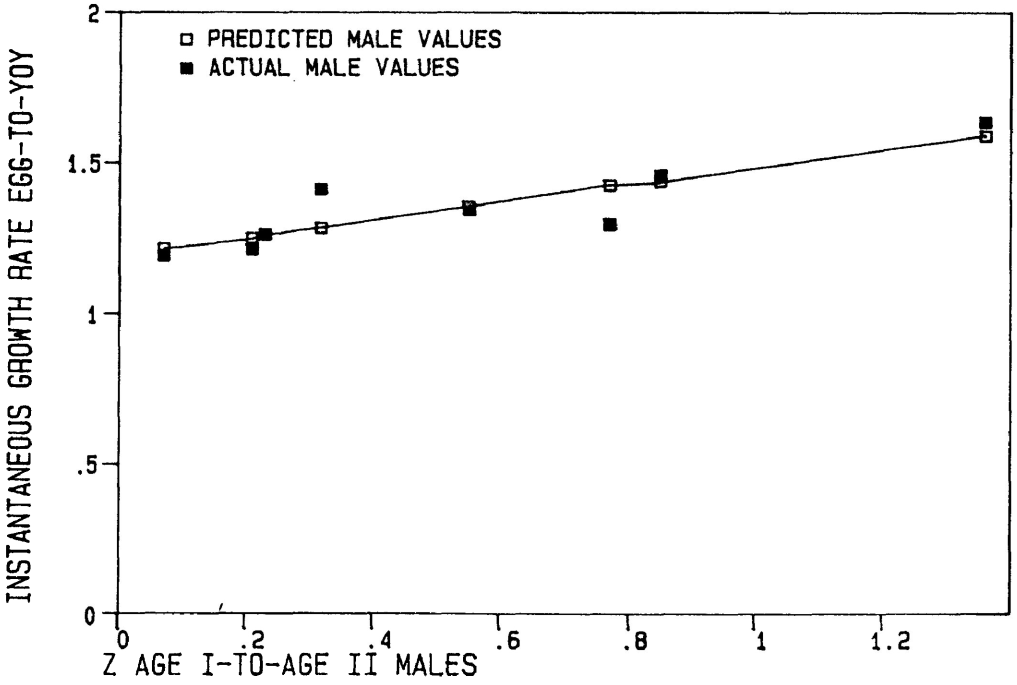
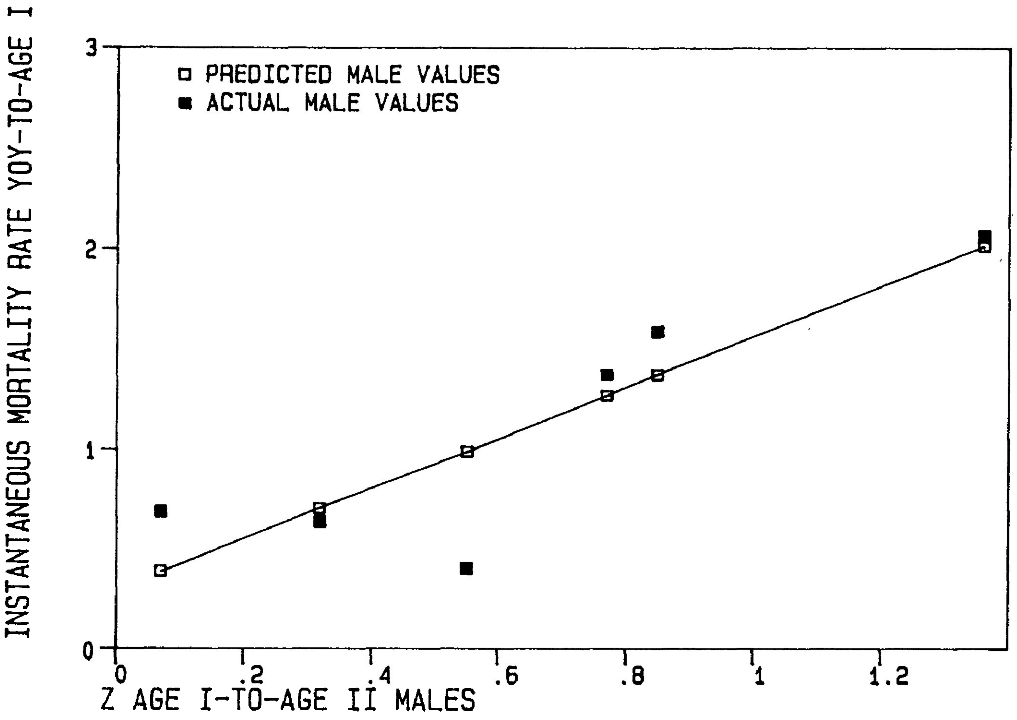
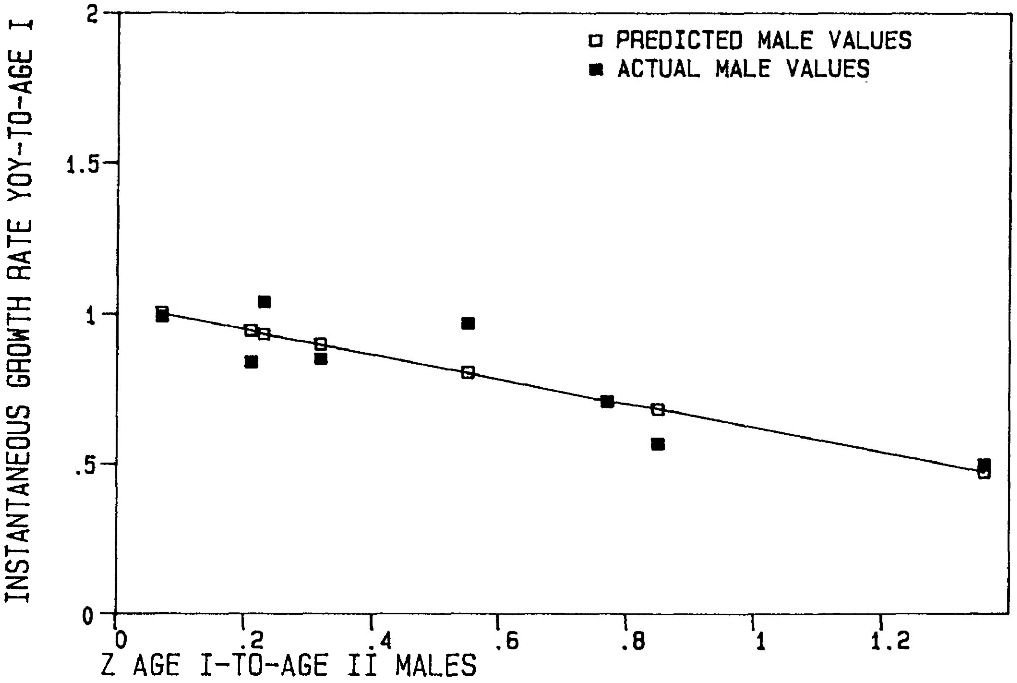

DOCK LAKE

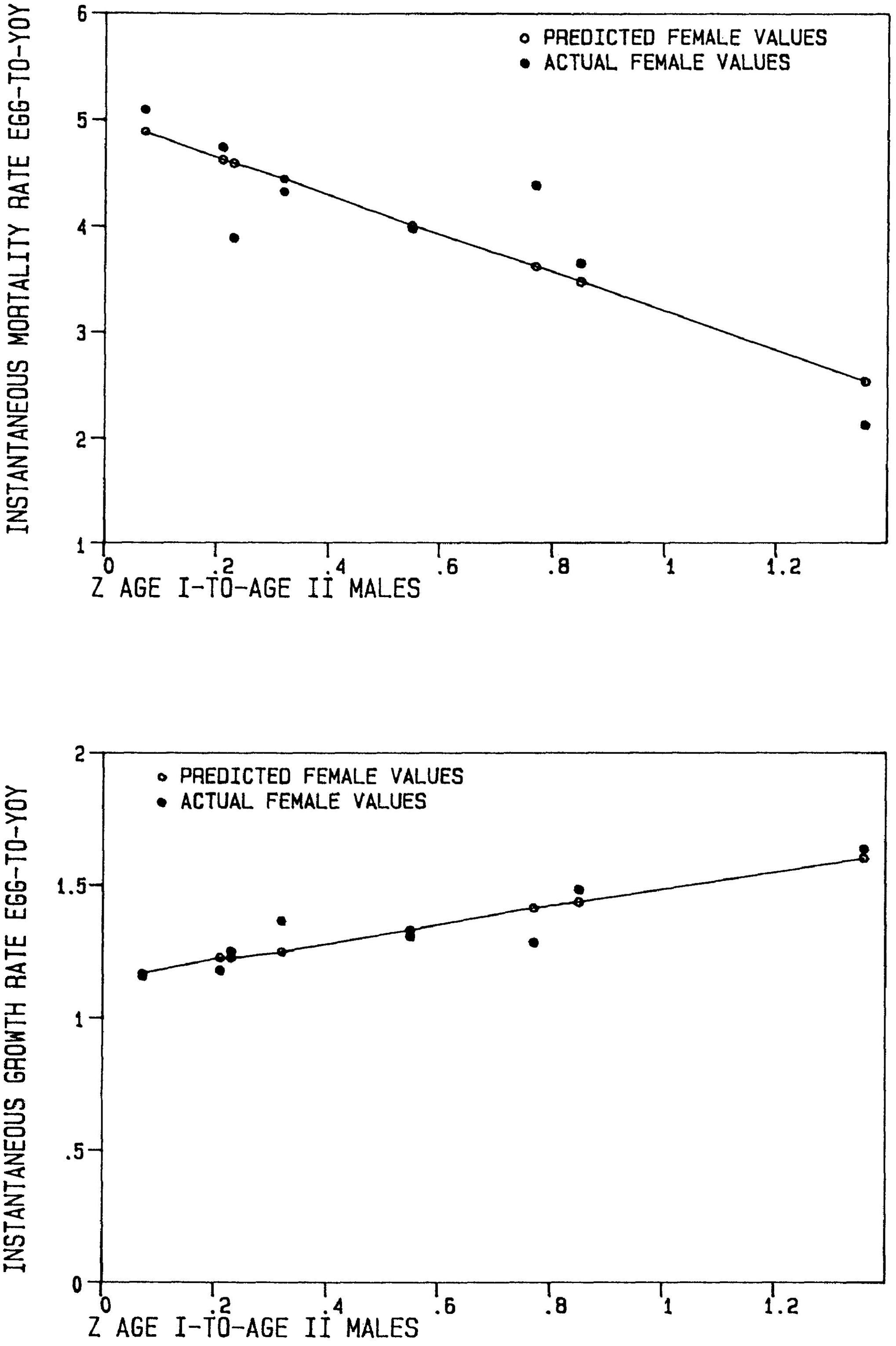
Figure 3. Relationships between male age I-to-age II total instantaneous mortality (Z) and male and female hatching-to-YOY and YOY-to-age I Z and instantaneous growth (G) in Shallow Lake. Shallow Lake regression lines, $Y=-1.802X+5.008$, $R2=0.78$ ($P<0.003$), and $Y=-1.814X+5.006$, $R2=0.76$ ($P<0.003$), for relationship between instantaneous mortality rate from egg-to-YOY (time t+1) (Y) and male instantaneous mortality rate from age I-to-age II (t) (X), for male and female crayfish, respectively; $Y=0.2996X+1.187$, $R2=0.78$ ($P<0.003$), and $Y=0.343X+1.148$, $R2=0.82$ ($P<0.002$), for relationship between instantaneous growth rate from egg-to-YOY (time t+1) and male instantaneous mortality rate from age I-to-age II (t) (X), for male and female crayfish, respectively; $Y=1.269X+0.2960$, $R2=0.77$ ($P<0.02$), and $Y=1.911X-0.2352$, $R2=0.83$ ($P<0.009$), for relationship between instantaneous mortality rate from YOY-to-age I (Y) and male instantaneous mortality rate from age I-to-age II (Y), for male and female crayfish, respectively; $Y=-0.4085X+1.025$, $R2=0.77$ ($P<0.003$), and $Y=-0.4357X+0.9650$, $R2=0.77$ ($P<0.003$), for relationship between instantaneous growth rate from YOY-to-age I (Y) and male instantaneous mortality rate from age I-to-age II (X), for male and female crayfish, respectively.


SHALLOW LAKE MALES
□ PREDICTED MALE VALUES
■ ACTUAL MALE VALUES
INSTANTANEOUS MORTALITY RATE EGG-TO-YOY
Z AGE I-TO-AGE II MALES
6
5
4
3
2
1
0
.2
.4
.6
.8
1
1.2

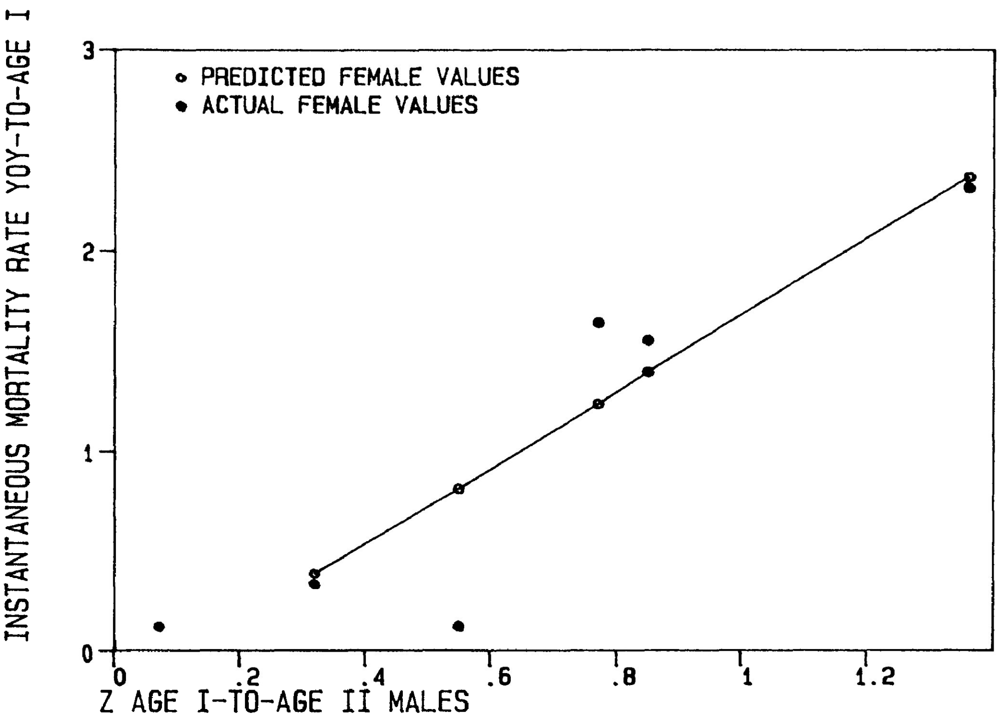

□ PREDICTED MALE VALUES
■ ACTUAL MALE VALUES
INSTANTANEOUS GROWTH RATE EGG-TO-YOY
Z AGE I-TO-AGE II MALES
2
1.5
1
.5
0
0
.2
.4
.6
.8
1
1.2

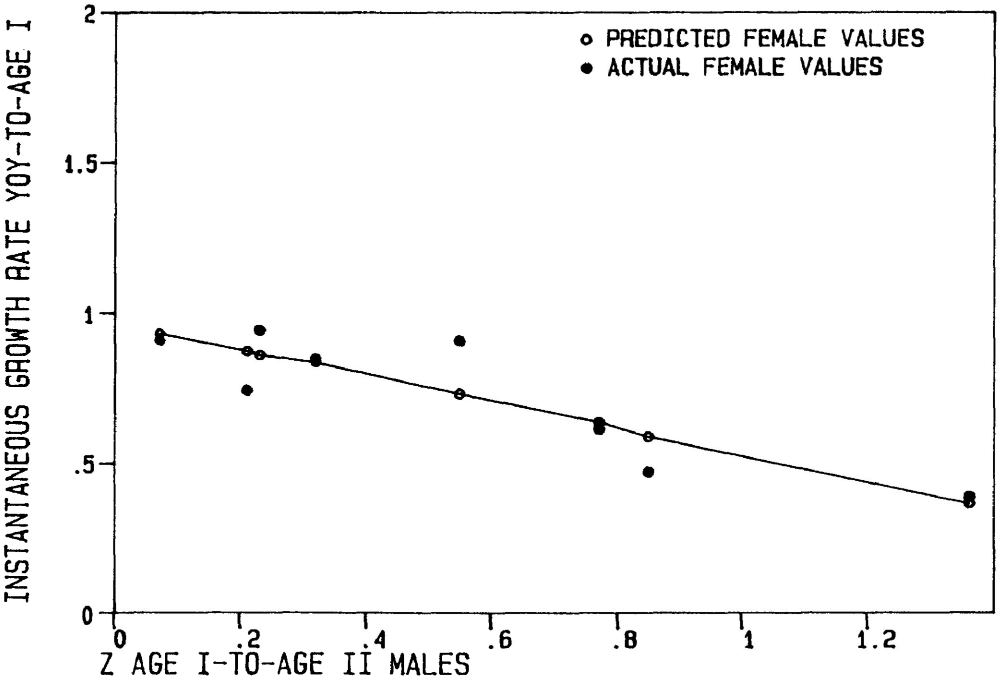

INSTANTANEOUS MORTALITY RATE YOY-TO-AGE I
3
2
1
0
□ PREDICTED MALE VALUES
■ ACTUAL MALE VALUES
0
.2
.4
.6
.8
1
1.2
Z AGE I-TO-AGE II MALES


INSTANTANEOUS GROWTH RATE YOY-TO-AGE I
2
1.5
1
.5
0
□ PREDICTED MALE VALUES
■ ACTUAL MALE VALUES
0
.2
.4
.6
.8
1
1.2
Z AGE I-TO-AGE II MALES



SHALLOW LAKE FEMALES


INSTANTANEOUS MORTALITY RATE YOY-TO-AGE I
○ PREDICTED FEMALE VALUES
● ACTUAL FEMALE VALUES
0
1
2
3
0
.2
.4
.6
.8
1
1.2
Z AGE I-TO-AGE II MALES


INSTANTANEOUS GROWTH RATE YOY-TO-AGE I
○ PREDICTED FEMALE VALUES
● ACTUAL FEMALE VALUES
0
.5
1
1.5
2
0
.2
.4
.6
.8
1
1.2
Z AGE I-TO-AGE II MALES

age II density on hatchling sex-specific growth and mortality rates. While growth of Shallow Lake hatchling males and females is inversely effected by male age II density, mortality in contrast is positively correlated (Fig. 1).

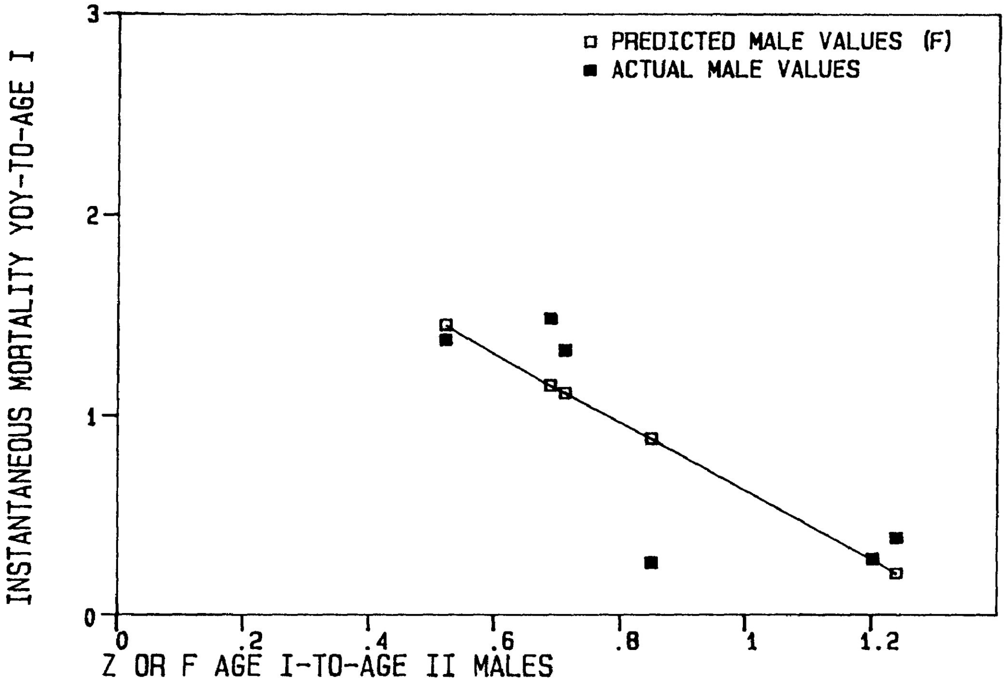
Although age II density is implicated, the actual mechanism must involve changes in age-specific mortality rates during the prereproductive-to-sexually mature life stage of males. Males mature between age I and age II. Maturing males influence adjustments in immature life stage population parameters (i.e., regulates). This is seen in Shallow Lake where YOY production rises with an increase in mortality between age I and age II (Fig. 2). Therefore the relationships between adult male mortality and other age- and sex-specific rates were also investigated.

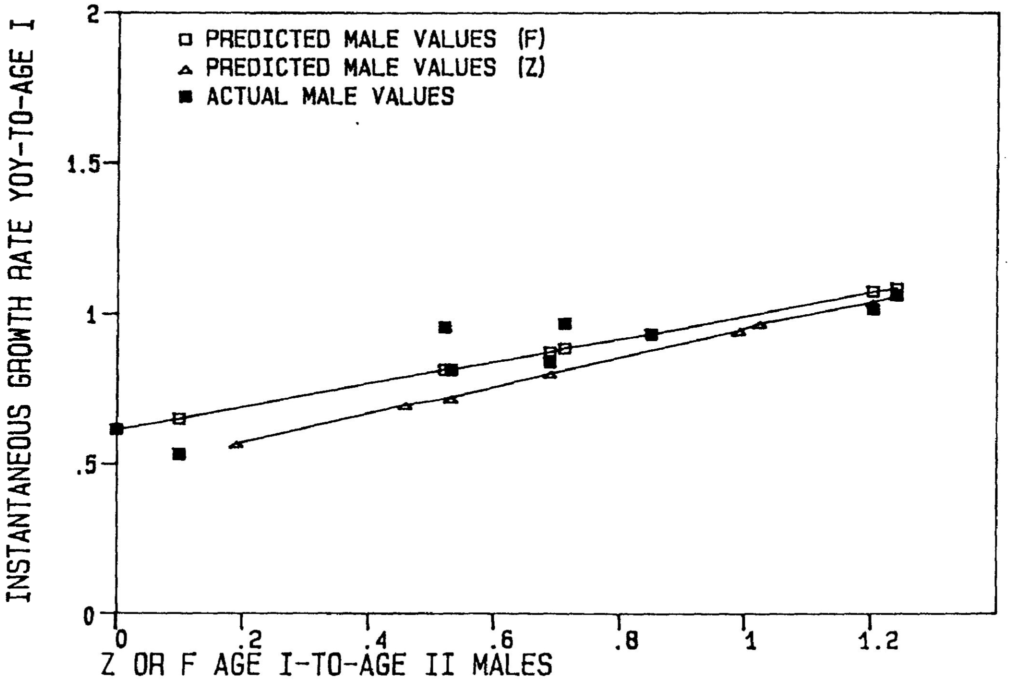
Shallow Lake male and female hatchling growth rates increase while their mortality rates decrease with a rise in male adult mortality rates (Fig. 3). Furthermore although Shallow Lake juvenile male and female growth decreases with an increase in adult male mortality, male and female juvenile mortality proportionally increases (Fig. 3).

The possible effect of age II male density and maturing male mortality on the growth and mortality of early life stages was also examined in the exploited Dock Lake population. This facilitated the separation of active biological processes from human activities. In Dock Lake YOY recruitment is independent of age II male density and adult male mortality (Fig. 1 and 2, respectively). After effort increased to 1350 trap-days in Dock Lake, male and female hatchling mortality became positively

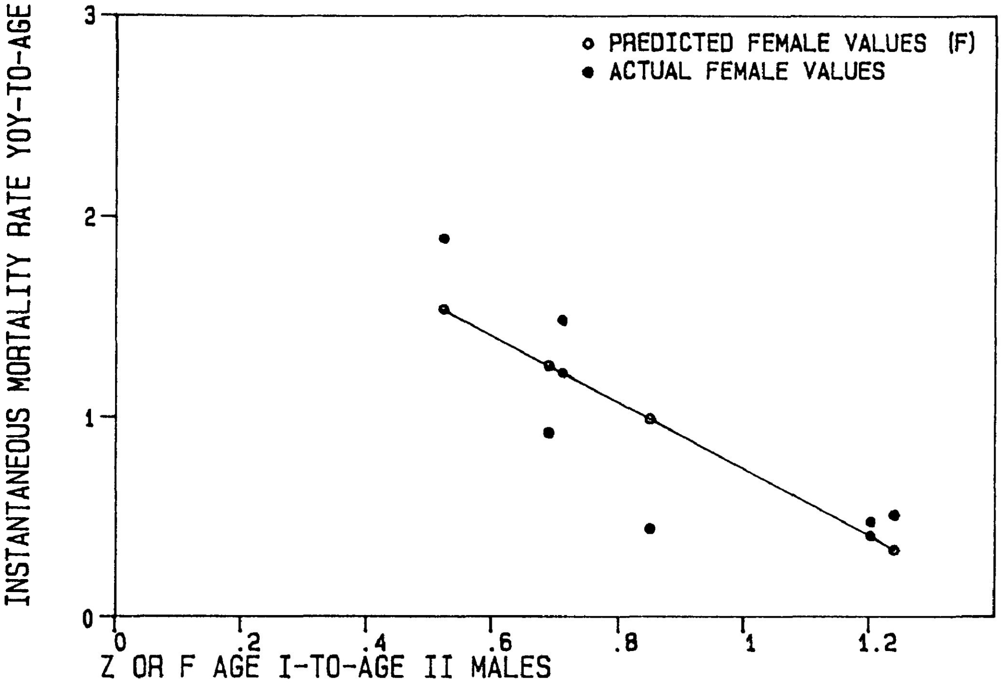
Figure 4. Relationships between male age I-to-age II total instantaneous mortality (Z) and fishing mortality (F), and male and female YOY-to-age I Z and instantaneous growth (G) in Dock Lake. Dock Lake regression lines, $Y=-1.689X+2.318$, $R2=0.68$ ($P<0.04$), and $Y=-1.677X+2.410$, $R2=0.65$ ($P<0.05$), for relationship between instantaneous mortality rate from YOY-to-age I (Y) and male fishing mortality from age I-to-age II (Y), for male and female crayfish, respectively; $Y=0.3847X+0.6071$, $R2=0.82$ ($P<0.0004$), and $Y=0.3826X+0.5973$, $R2=0.82$ ($P<0.0004$), for relationship between instantaneous growth rate from YOY-to-age I (X) and male fishing mortality rate from age I-to-age II (Y), for male and female crayfish, respectively; $Y=0.4824X+0.4649$, $R2=0.93$ ($P<0.0001$), and $Y=0.4719X+0.4623$, $R2=0.89$ ($P<0.0001$), for relationship between instantaneous growth rate from YOY-to-age I (Y) and male instantaneous mortality rate from age I-to-age II (X), for male and female crayfish respectively.

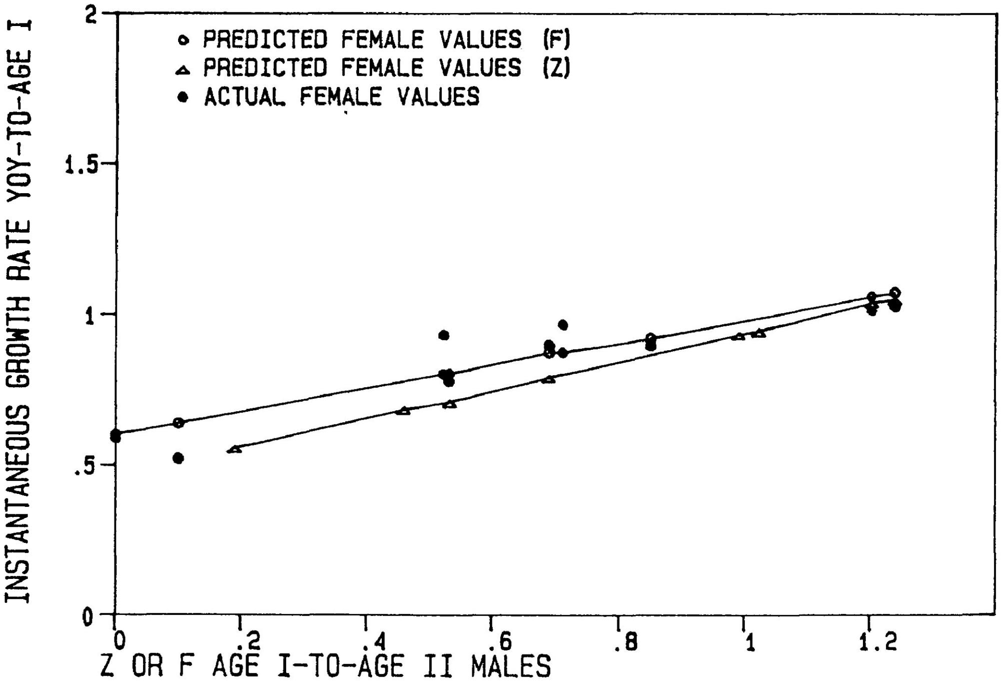
DOCK LAKE MALES





DOCK LAKE FEMALES





related to the density of age II males (Fig. 1), while hatchling growth was uncorrelated. No relationship is seen between male adult mortality and hatchling growth or mortality. It is as if harvesting enervates the maturing male life stage mechanism (i.e., age I-to-age II male mortality) regulating hatchling growth and mortality. However, in Dock Lake density-dependent mortality of male and female hatchlings remains unaffected by fishing efforts up to 4000 trap-days.

In Dock Lake exploitation dramatically altered relationships between growth and mortality rates among life stages. At efforts of 2600 trap-days and greater fishing accounts for all of the estimated total annual mortality experienced by the population (i.e., Z=F). Thus harvesting is the primary mortality factor for nearly all adult male crayfish. Increased age I-to-age II male mortality is associated with: (1) decreases in male and female juvenile mortality (Fig. 4) and, (2) increases in juvenile male and female growth (Fig. 4). Juvenile growth and mortality relationships in Dock Lake are thus the antitheses of Shallow Lake's.

Production of YOY in Dock Lake is unrelated to these growth-mortality interrelationships. Yet hatchling male and female mortality is regulated by age II male density interactions (Fig. 1). Recruitment to the exploitable stock is therefore associated with two processes and especially their related time lags. Hatchling mortality relates to the density of surviving age II males remaining from the previous years exploitation of age I males (Fig. 1). Juvenile recruitment in turn depends upon the current level of male age I fishing mortality (Fig. 4).

Figure 5. Disparity between age I and age II male sex ratio for 1975 to 1983 cohorts in Dock and Shallow Lake.

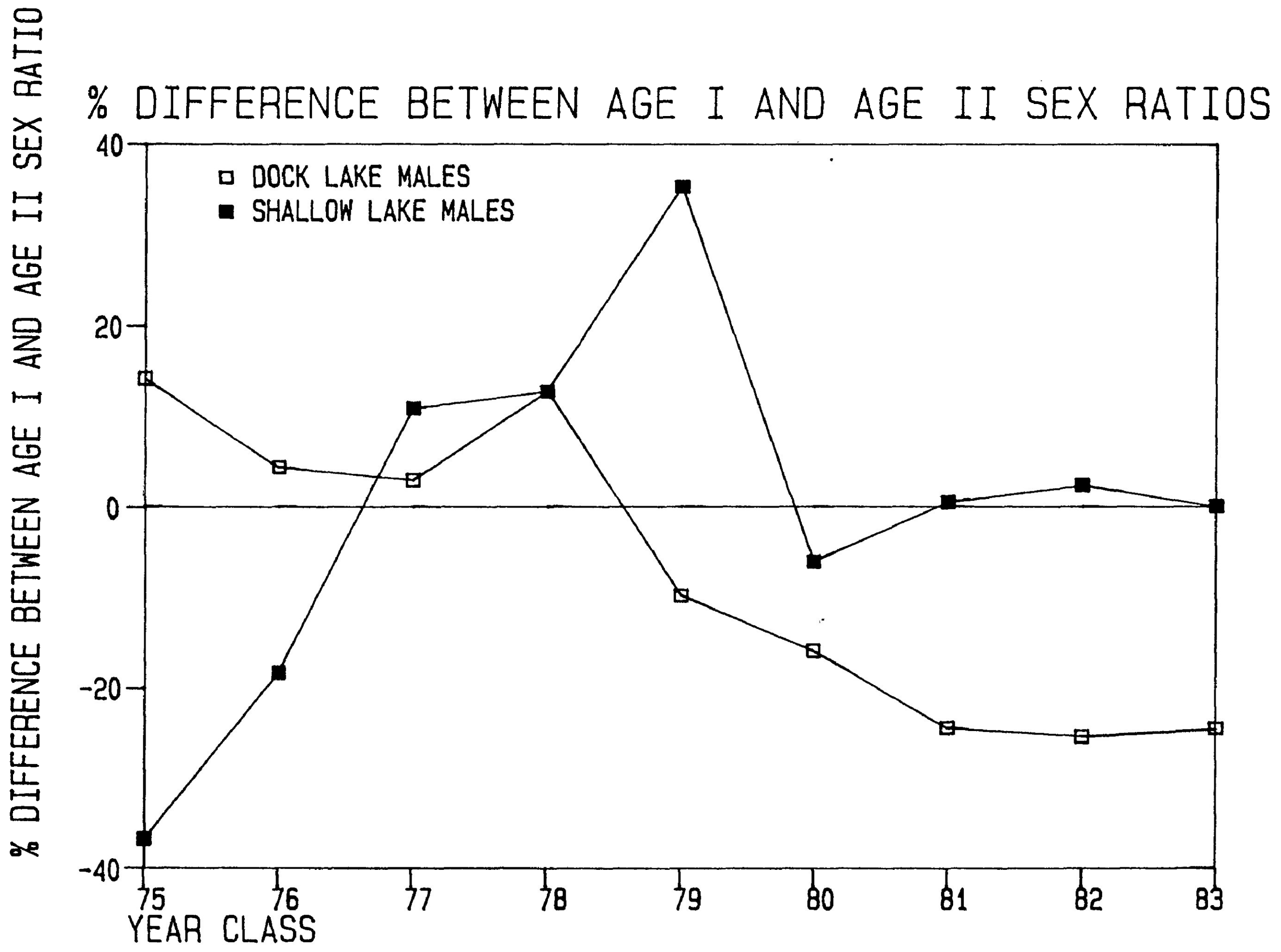

% DIFFERENCE BETWEEN AGE I AND AGE II SEX RATIOS
□ DOCK LAKE MALES
■ SHALLOW LAKE MALES
% DIFFERENCE BETWEEN AGE I AND AGE II SEX RATIO
40
20
0
-20
-40
75
76
77
78
79
80
81
82
83
YEAR CLASS

Figure 6. Relationships between percent female sex ratio related to population density in Dock and Shallow Lake 1976 to 1985. Shallow Lake regression line, Y=0.00353X+38.34695, R2=0.72 (P<0.001), for relationship between percentage female in population (Y) and exploitable stock density (age I+) (X). Regression of similar relationship in Dock Lake was not significant, average percent female composition=52.2% (standard error=0.86).

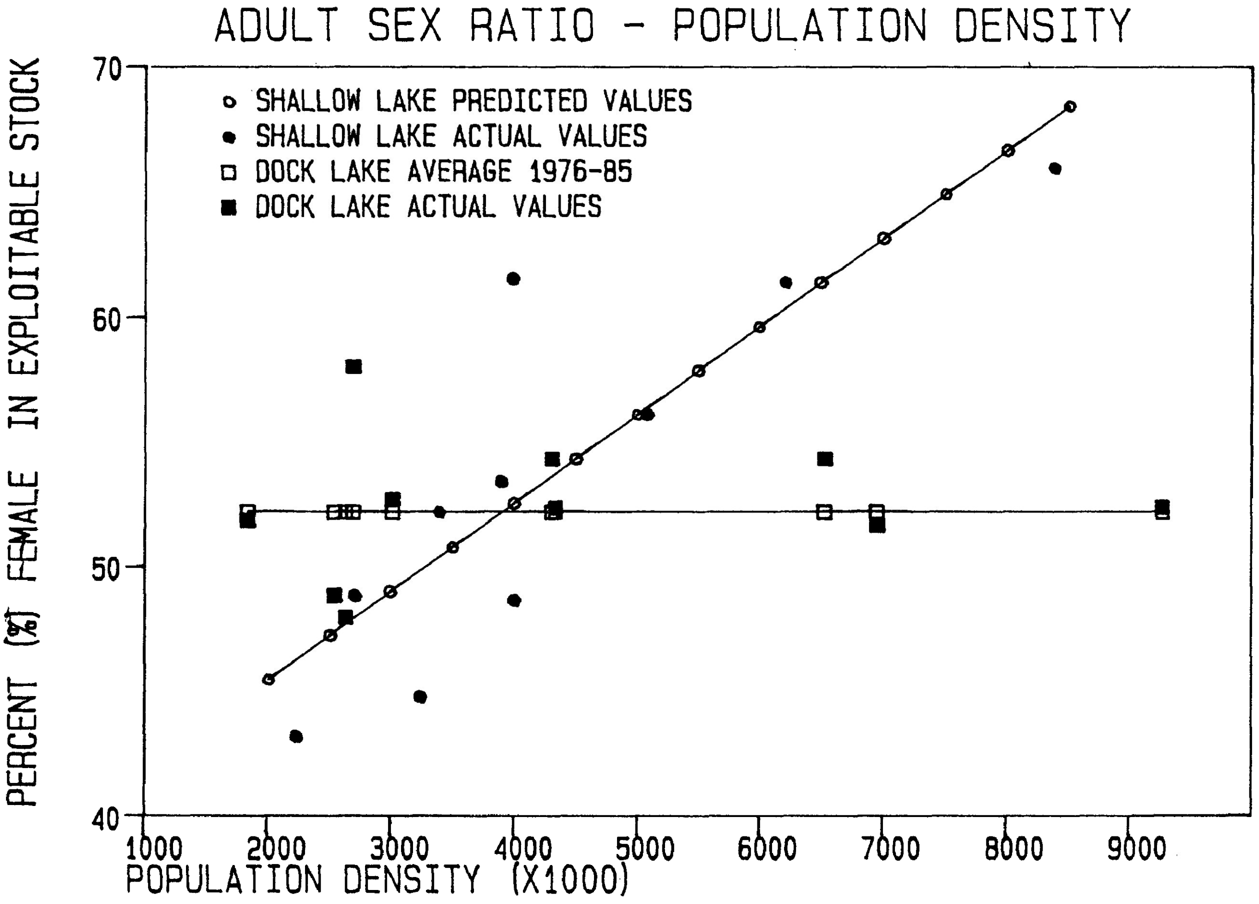

ADULT SEX RATIO - POPULATION DENSITY
○ SHALLOW LAKE PREDICTED VALUES
● SHALLOW LAKE ACTUAL VALUES
□ DOCK LAKE AVERAGE 1976-85
■ DOCK LAKE ACTUAL VALUES
PERCENT (%) FEMALE IN EXPLOITABLE STOCK
70
60
50
40
1000
2000
3000
4000
5000
6000
7000
8000
9000
POPULATION DENSITY (X1000)

Table 1. Shallow Lake population estimates by age and sex, 1976 to 1985.

TABLE 1. Shallow Lake population estimates by age and sex, 1976 to 1985.

Year	Age-Class							
	Male				Female			
	I	II	III	Total	I	II	III	Total
1976	1137	225	25	1387	594	714	16	1324
1977	940	292	38	1270	516	411	38	965
1978	1188	400	39	1627	1344	357	69	1770
1979	1212	551	27	1790	888	508	60	1456
1980	1348	699	8	2055	1546	374	30	1950
1981	796	981	34	1811	1486	575	18	2079
1982	846	646	46	1538	1030	1324	98	2452
1983	1245	790	368	2403	1904	952	947	3803
1984	1215	989	33	2237	1222	1451	167	2840
1985	1507	1215	128	2850	4225	1222	96	5543

Table 2. Dock Lake population estimates and harvests by age and sex, 1976 to 1985.

TABLE 2. Dock Lake population estimates and harvests by age and sex, 1976 to 1985.

Year	Age-Class							
	Male				Female			
	I	II	II	Total	I	II	III	Total
1976	609	268	8	885	627	294	29	950
1977	958	383	27	1368	949	299	14	1262
	(89)[1]	(45)	(1)	(135)	(42)	(20)	(-)	(62)
1978	1260	796	8	2064	1503	724	43	2270
	(642)	(225)	(1)	(868)	(397)	(227)	(12)	(636)
1979	934	469	17	1420	1013	533	39	1585
	(377)	(139)	(3)	(519)	(255)	(266)	(14)	(535)
1980	932	336	33	1301	947	286	9	1242
	(463)	(169)	(12)	(644)	(367)	(133)	(9)	(509)
1981	629	469	33	1131	951	580	30	1561
	(258)	(197)	(33)	(488)	(214)	(223)	(17)	(454)
1982	1650	371	39	2060	1463	737	40	2240
	(1155)	(263)	(28)	(1446)	(710)	(407)	(21)	(1138)
1983	2402	495	88	2985	2736	738	75	3549
	(1709)	(386)	(37)	(2132)	(1258)	(312)	(69)	(1639)
1984	2606	693	56	3355	2157	1290	147	3594
	(1490)	(391)	(41)	(1922)	(638)	(441)	(49)	(1128)
1985	3402	970	38	4410	3445	1383	35	4863
	(2448)	(798)	(38)	3284	(1480)	(763)	(31)	(2274)

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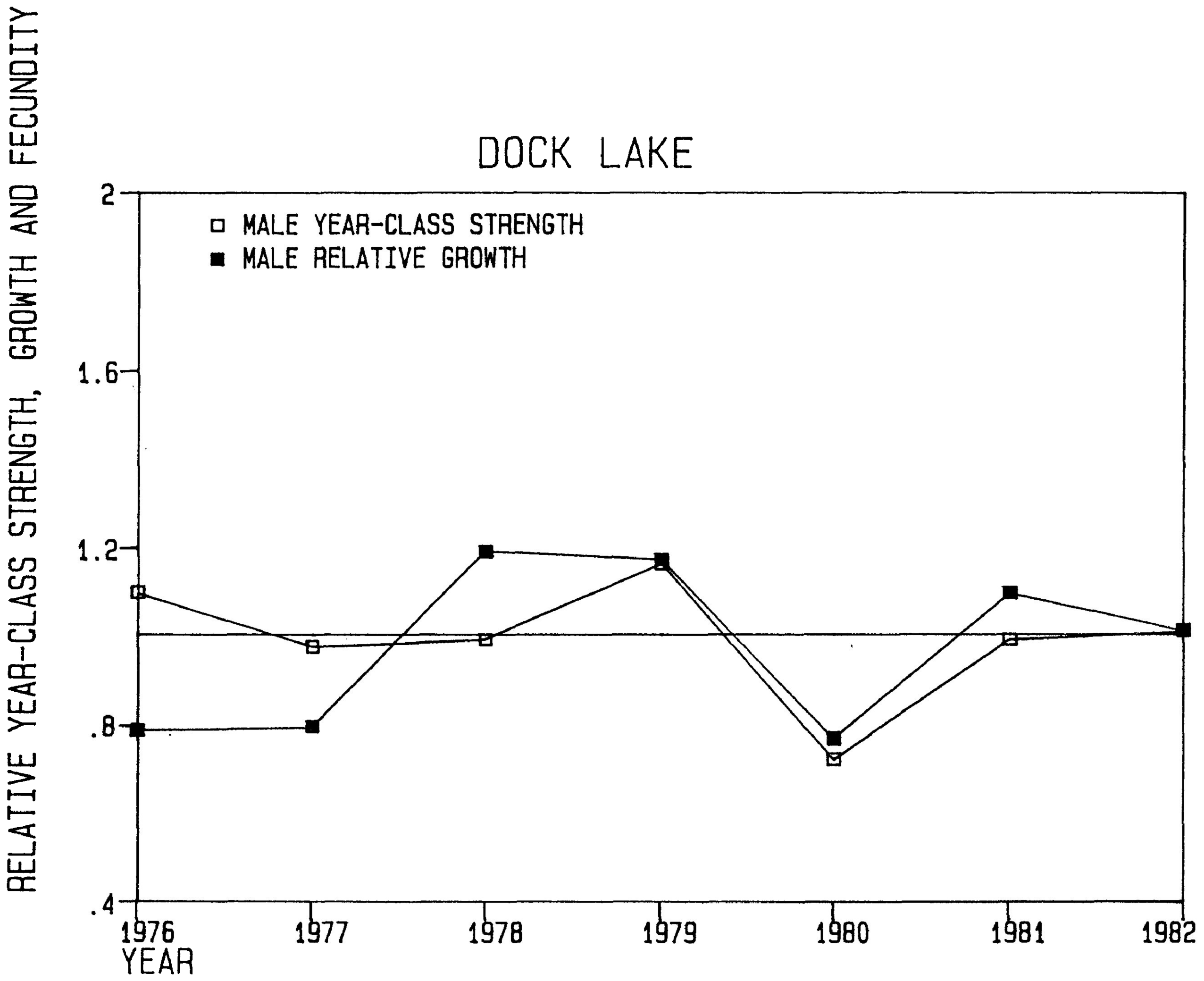
[1] Number of crayfish harvested

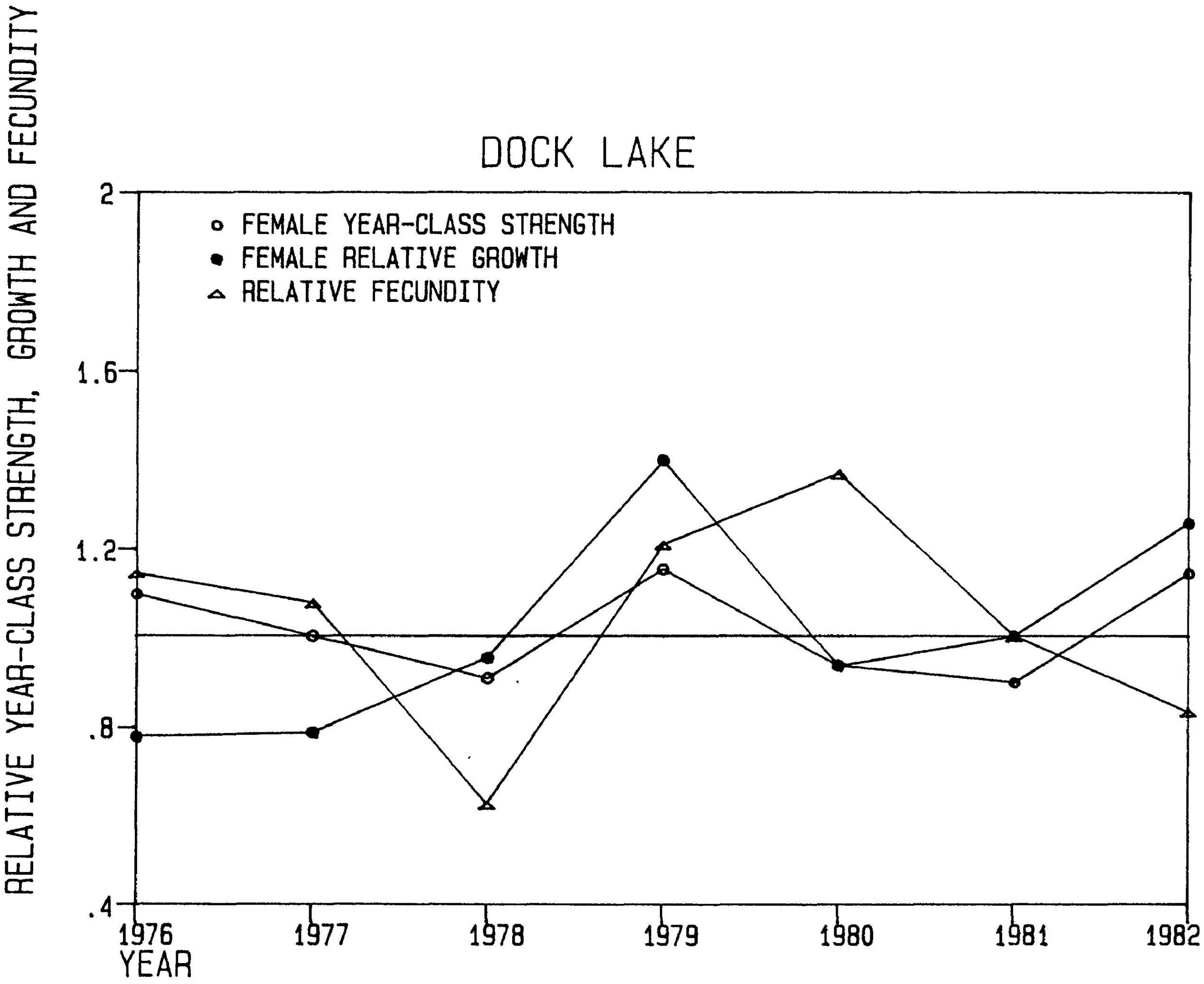
Increased exploitation shifts the male sex ratios between maturing juvenile (age I) and fully mature (age II) sub-populations. The disparity between age I and age II male sex ratios in Dock Lake increased with increasing effort (i.e., differential fishing mortality at age I) (Fig. 5). During the same period differences between age I and age II male sex ratios in Shallow Lake stabilized (Fig. 5).

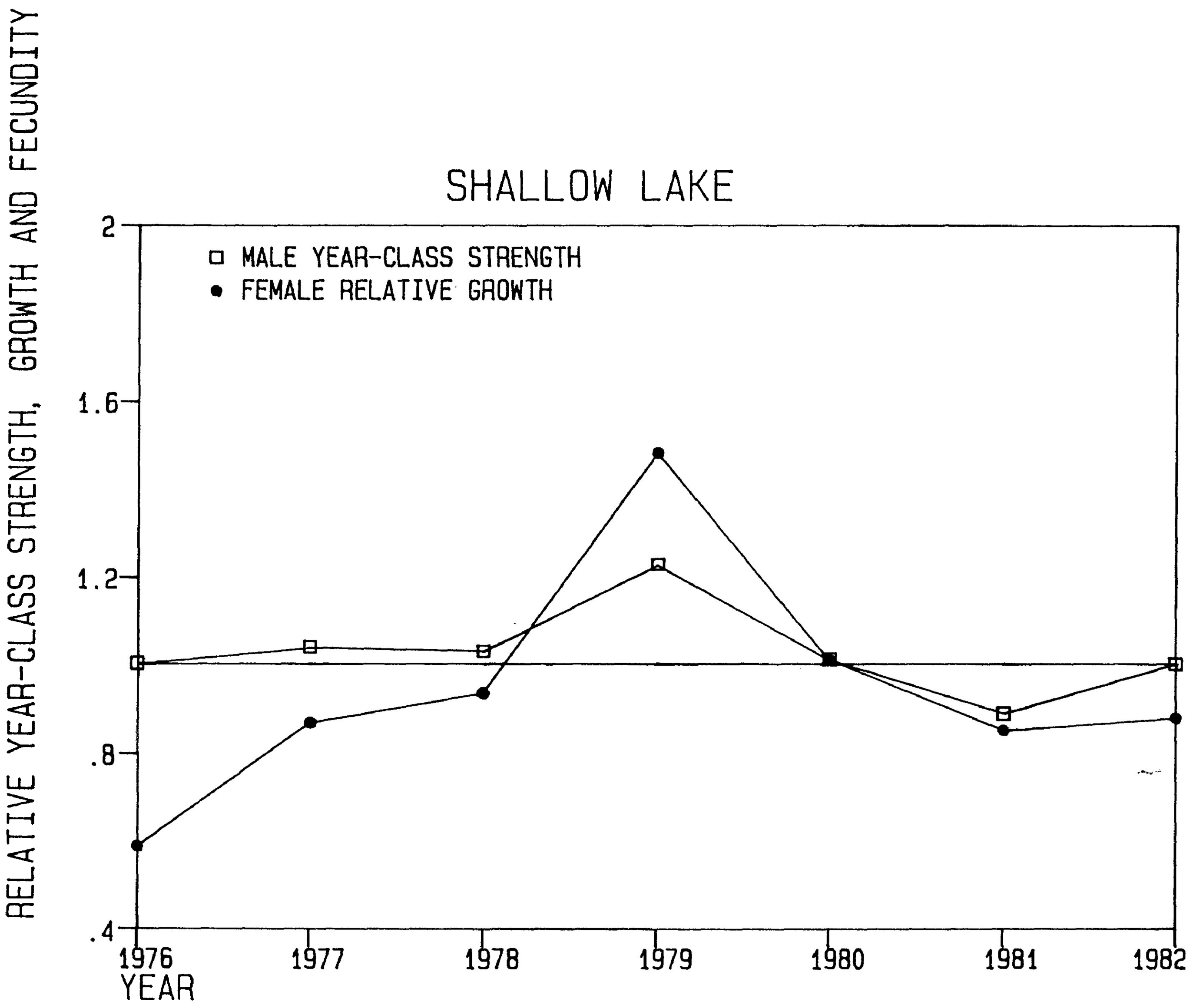
Exploitation also altered the relationship between exploitable stock density (age I and older) and sex ratio. At low densities (<0.50 crayfish.m$^{2.-1}$) males predominate in Shallow Lake but as density increases the sex ratio favours females (Table 1 and Fig. 6). By 1985, Shallow Lake density increased to 1.04 crayfish.m$^{2.-1}$ but the population was 66% females. In contrast Dock Lake maintained a stable sex ratio (52.2% females, standard deviation = 2.73, n=10) even at high densities (Table 2 and Fig. 6).

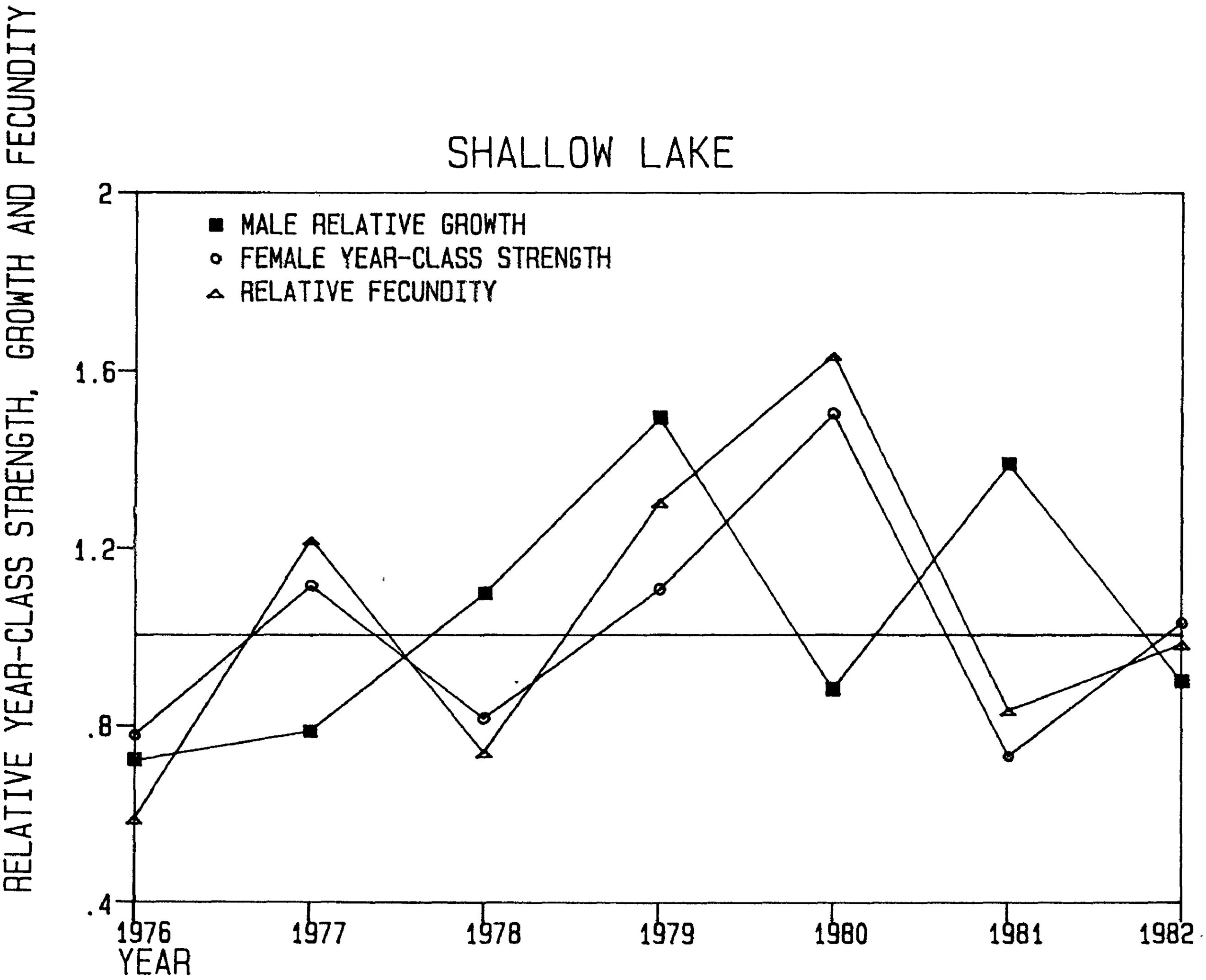
Adjustments in: male age I-to-age II sex ratios, growth and mortality rates ultimately regulate population density. The effect of male regulation is mediated through changes in relative year-class strength, relative growth and relative egg production. Relative year-class strength refers to the cohort produced in that year. Relative growth alludes to the mean change in size experienced by the existing age structure during that particular year. Relative egg production in turn is the average lifetime reproductive output of the cohort born in that year. In Shallow Lake while male year-class strength is proportional to female relative growth, female relative year-class strength is inversely related to male relative growth (Fig. 7). Also Shallow Lake male

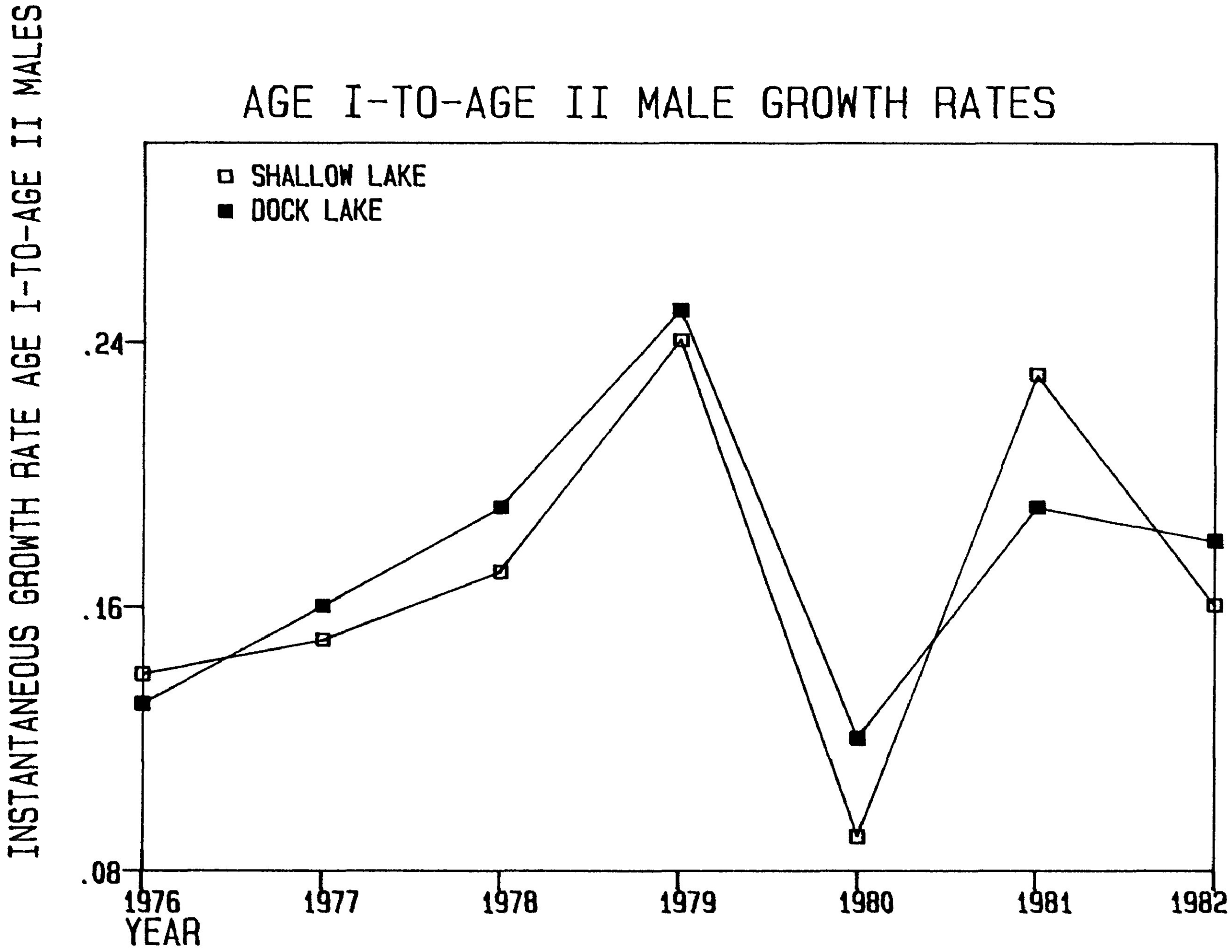
Figure 7. Relative year-class strength, annual growth, cohort egg production and male age I-to-age II instantaneus growth (G) for Dock and Shallow Lake 1976 to 1982 cohorts.


DOCK LAKE
□ MALE YEAR-CLASS STRENGTH
■ MALE RELATIVE GROWTH
RELATIVE YEAR-CLASS STRENGTH, GROWTH AND FECUNDITY
2
1.6
1.2
.8
.4
1976
1977
1978
1979
1980
1981
1982
YEAR


DOCK LAKE
○ FEMALE YEAR-CLASS STRENGTH
● FEMALE RELATIVE GROWTH
△ RELATIVE FECUNDITY
RELATIVE YEAR-CLASS STRENGTH, GROWTH AND FECUNDITY
2
1.6
1.2
.8
.4
1976
1977
1978
1979
1980
1981
1982
YEAR


SHALLOW LAKE
□ MALE YEAR-CLASS STRENGTH
● FEMALE RELATIVE GROWTH
RELATIVE YEAR-CLASS STRENGTH, GROWTH AND FECUNDITY
2
1.6
1.2
.8
.4
1976
1977
1978
1979
1980
1981
1982
YEAR


SHALLOW LAKE
■ MALE RELATIVE GROWTH
○ FEMALE YEAR-CLASS STRENGTH
△ RELATIVE FECUNDITY
RELATIVE YEAR-CLASS STRENGTH, GROWTH AND FECUNDITY
2
1.6
1.2
.8
.4
1976
1977
1978
1979
1980
1981
1982
YEAR



AGE I-TO-AGE II MALE GROWTH RATES
□ SHALLOW LAKE
■ DOCK LAKE
INSTANTANEOUS GROWTH RATE AGE I-TO-AGE II MALES
.24
.16
.08
1976
1977
1978
1979
1980
1981
1982
YEAR

Figure 8. Relationship between male and female instantaneous growth rate (G) and instantaneous mortality rate (Z) during the egg-to-young-of-year (YOY) life stage of Dock and Shallow Lake crayfish 1976-1985. Shallow Lake regression lines, $Y=-6.005X+12.22$, $R2=0.95$ ($P<0.0001$), and $Y=-5.168X+10.95$, $R2=0.90$ ($P<0.0001$), for relationship between instantaneous mortality rate from egg-to-YOY (Y) and instantaneous growth rate from egg-to-YOY (X), for male and female crayfish, respectively. Dock Lake regression lines (excluding 1985 data), $Y=-2.098X+6.039$, $R2=0.87$ ($P<0.0002$), and $Y=-1.153X+4.663$, $R2=0.51$ ($P<0.02$), for relationship between instantaneous mortality rate from egg-to-YOY (Y) and instantaneous growth rate from egg-to-YOY (X), for male and female crayfish, respectively.

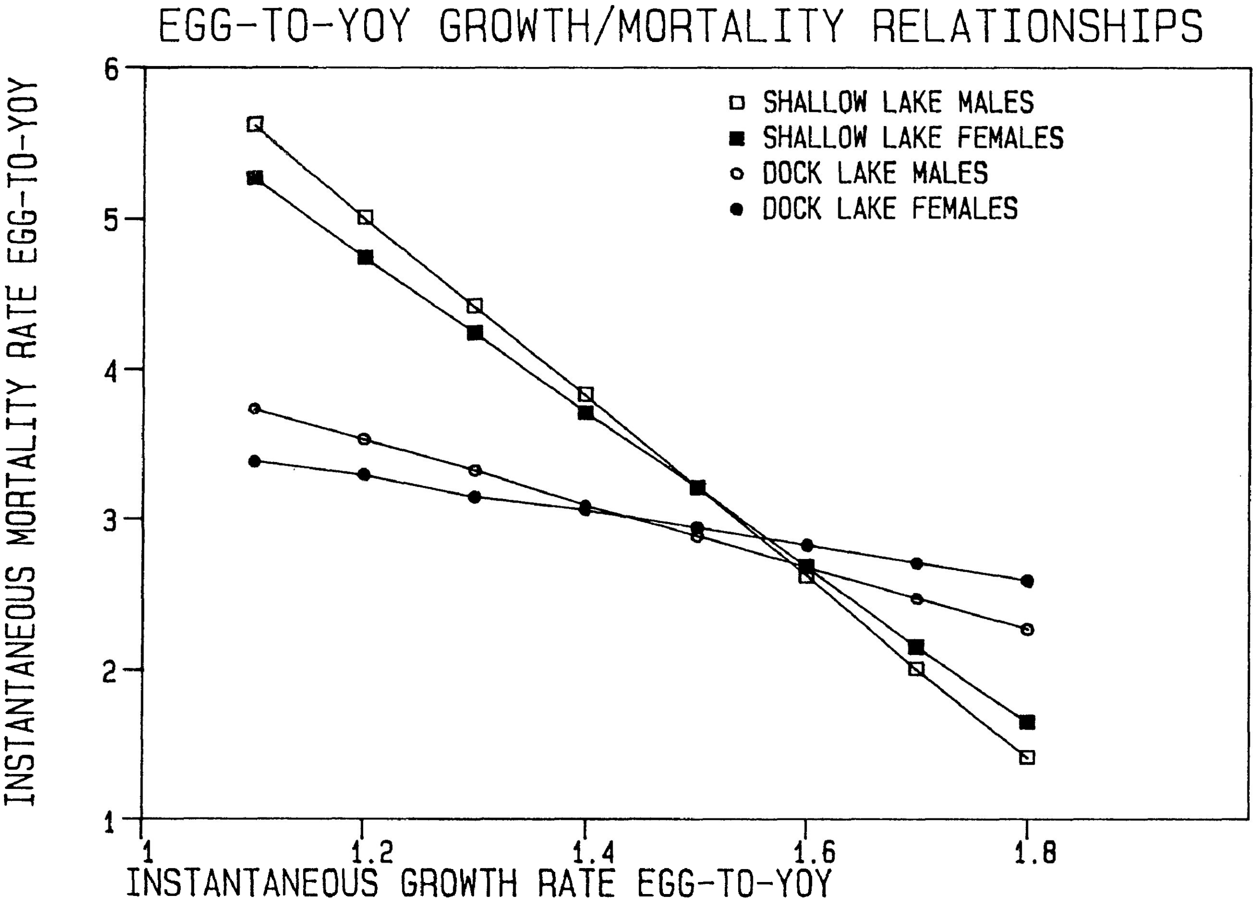
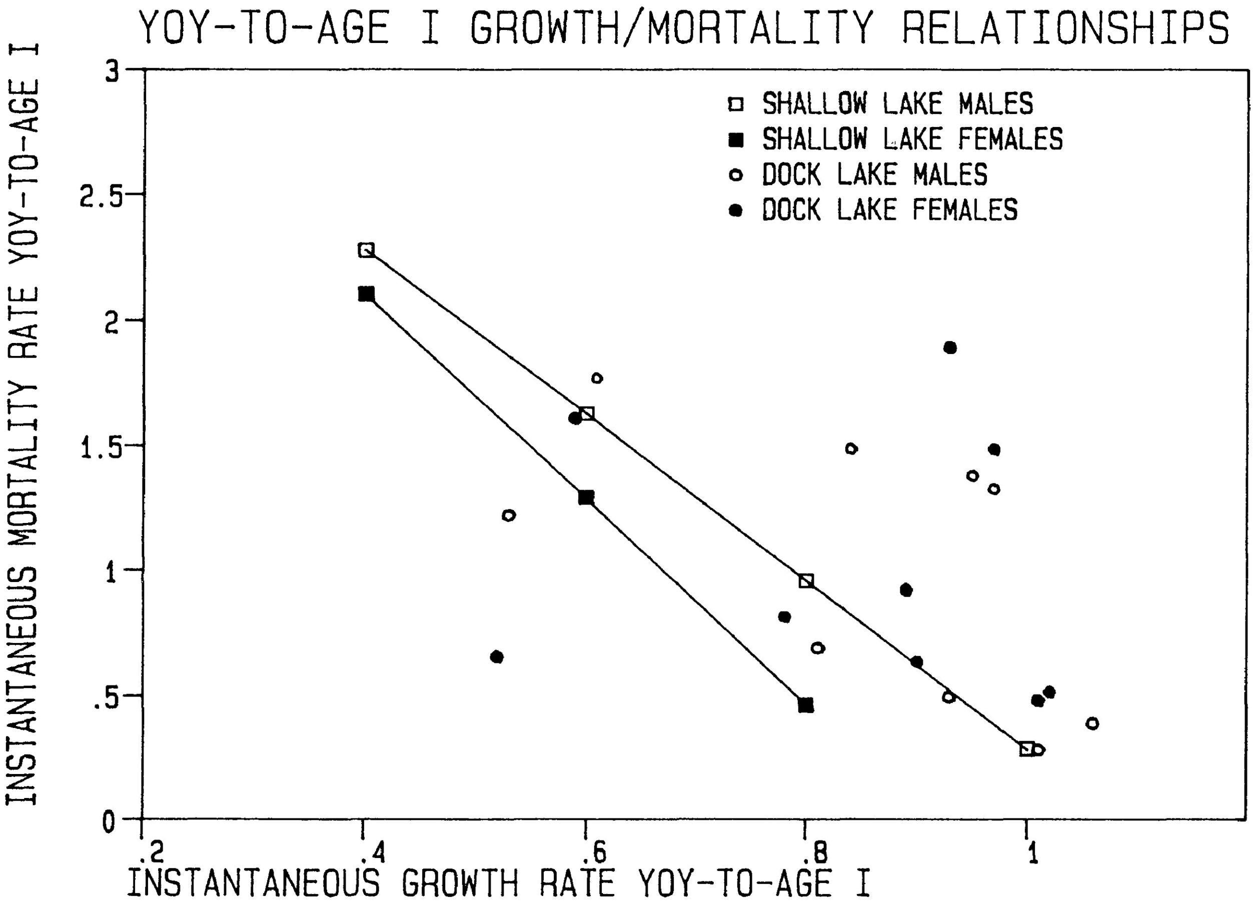

EGG-TO-YOY GROWTH/MORTALITY RELATIONSHIPS
□ SHALLOW LAKE MALES
■ SHALLOW LAKE FEMALES
○ DOCK LAKE MALES
● DOCK LAKE FEMALES
INSTANTANEOUS MORTALITY RATE EGG-TO-YOY
6
5
4
3
2
1
1
1.2
1.4
1.6
1.8
INSTANTANEOUS GROWTH RATE EGG-TO-YOY

Figure 9. Relationship between male and female instantaneous growth rate (G) and instantaneous mortality rate (Z) during the young-of-year (YOY)-to-age I life stage of Shallow Lake crayfish 1976-1985. Shallow Lake regression lines, $Y=-3.321X+3.609$, R2=0.90 ($P<0.0001$), and $Y=-4.096X+3.741$, R2=0.91 ($P<0.0001$), for relationship between instantaneous mortality rate form YOY-to-age I (Y) and instantaneous growth rate from YOY-to-age I (X), for male and female crayfish, respectively.

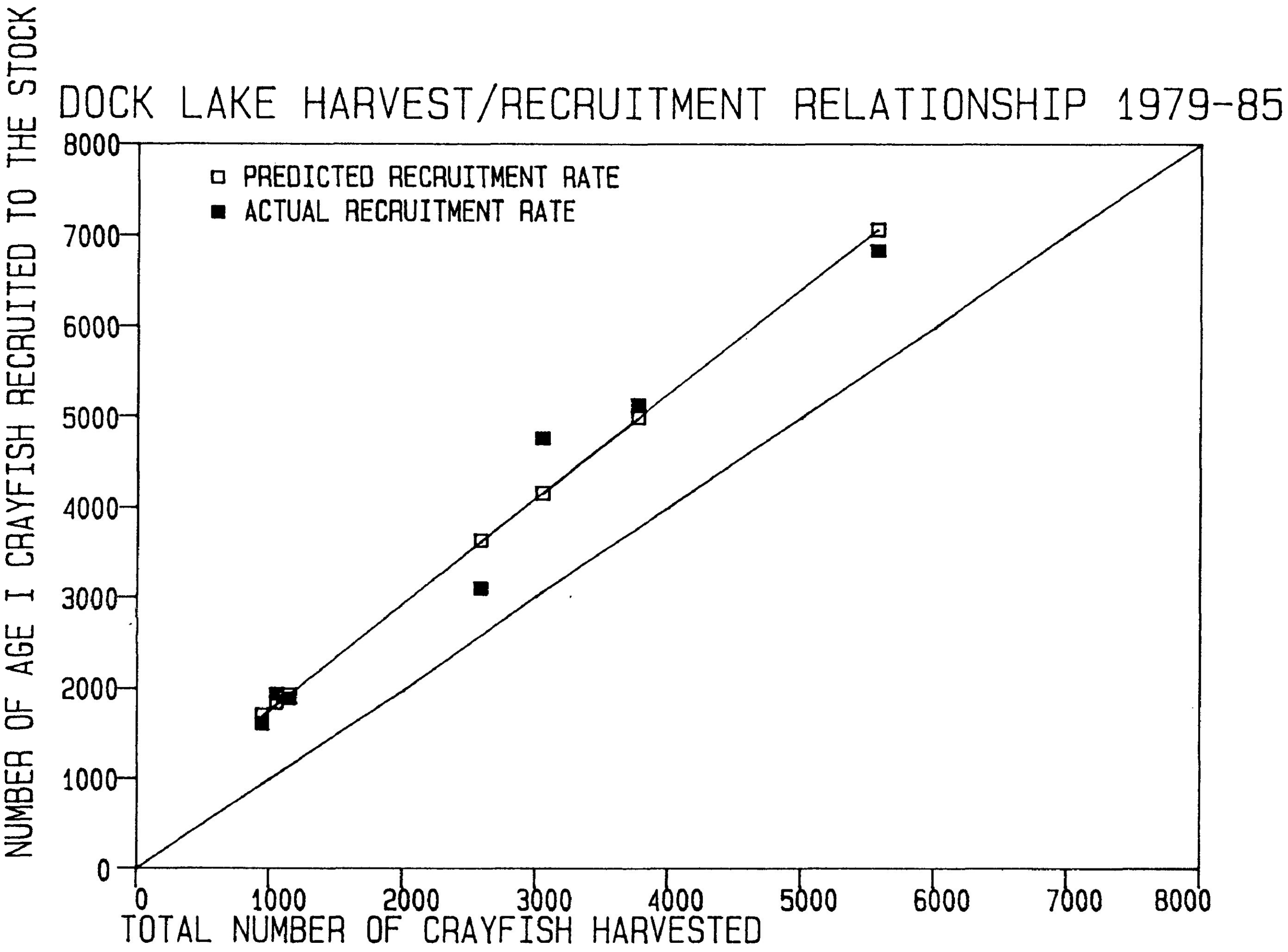

YOY-TO-AGE I GROWTH/MORTALITY RELATIONSHIPS
□ SHALLOW LAKE MALES
■ SHALLOW LAKE FEMALES
○ DOCK LAKE MALES
● DOCK LAKE FEMALES
INSTANTANEOUS MORTALITY RATE YOY-TO-AGE I
3
2.5
2
1.5
1
.5
0
.2
.4
.6
.8
1
INSTANTANEOUS GROWTH RATE YOY-TO-AGE I

relative annual growth is correlated to changes in the instantaneous growth rate of adult male crayfish (Fig. 7; Spearman rank correlation coefficent "rho' = 0.9821, P<0.05). This relationship has oscillated on a two year cycle. Shallow Lake relative egg production is proportional to female relative year-class strength (Fig. 7). In contrast, Dock Lake relative year-class strength and relative growth are positively correlated in males and females but relative egg production is independent of female relative year class strength (Fig. 7). Exploitation has thus displaced the feedback mechanism between annual male growth and female year-class strength, and male year-class strength and annual female growth. These relationships ordinarily cause a two year cyclic covariation between female abundance/cohort egg production and annual juvenile-to-sexually mature male growth as seen in the unexploited Shallow Lake population.

Juvenile Life Stage Dynamics.

Changes in male and female mortality rates are therefore related to growth rates experienced within juvenile life stages. Mortality inversely correlates with hatchling growth in both lakes, however, the relationship is more robust in the control lake (i.e., smaller decrease in growth results in increased mortality) (Fig. 8). Shallow Lake juvenile mortality and growth correlate in a similar fashion (Fig. 9). In contrast, Dock Lake juvenile mortality and growth are independent. Therefore regulation of growth/mortality life history characteristics endures over a longer portion of the life cycle in the unexploited population; resulting in a multistage recruitment

Figure 10. Relationship between total annual harvest and age I recruitment rate in Dock Lake 1979-1985. Dock Lake regression line, $Y=1.158X+612.8$, $R2=0.97$ ($P<0.0001$), for relationship between age I recruitment rate (Y) and number of crayfish harvested (X).


DOCK LAKE HARVEST/RECRUITMENT RELATIONSHIP 1979-85
□ PREDICTED RECRUITMENT RATE
■ ACTUAL RECRUITMENT RATE
NUMBER OF AGE I CRAYFISH RECRUITED TO THE STOCK
0
1000
2000
3000
4000
5000
6000
7000
8000
TOTAL NUMBER OF CRAYFISH HARVESTED
0
1000
2000
3000
4000
5000
6000
7000
8000

process. Exploitation in Dock Lake thus both diminishes hatchling growth/mortality interactions as well as eliminates juvenile growth/mortality interdependence.

Recruitment Dynamics of the Exploitable Stock

High yields in Dock Lake are the result of increased recruitment at age I of consistently large year-classes. Empirical evidence implies a density-dependent adjustment in YOY production and age I recruitment. Analysis of fecundity and YOY densities suggest YOY production to be at a maximum relative to available nursery habitat irregardless of population density, individual female fecundity or total egg production (Morgan 1987). Since annual YOY recruitment in Dock Lake remains constant, the critical life stage process determining year-class strength is natural juvenile mortality. This decreases with increasing fishing mortality of age I-to-age II males (Fig. 4). In terms of population regulation, the selective trap fishery functions as a density-dependent modifier by proportionately removing more age I males as the population increases. Since yields soon become dependent upon age I recruitment rates at increasing levels of fishing effort (e.g., 2600 trap-days and greater), changes in annual harvests serve as indicators of variations in recruitment/year-class strength to the exploitable stock (Fig. 10).

Compensatory changes occurred in the Dock Lake populations vital statistics to increase recruitment/year-class strength. In contrast, Shallow Lake year-class strength is determined by a sex-specific multistage recruitment process at the hatchling and juvenile stages. The intensity of the hatchling biotic feedback mechanism produces a tremendous variability in male and female YOY production (e.g., Shallow Lake coefficient of variation of YOY estimates 1976-1985: male = 73.8%; female = 67.7%). In contrast Shallow Lake potential year-class strength becomes further modified by differential density-dependent juvenile mortality. This self-regulating mechanism results in a numerically stable male age I recruitment rate (e.g., Shallow Lake 1976-1985 average male age I recruitment = 1143, standard deviation = 222.8, coefficient of variation of male age I recruitment = 19.5%). In contrast female recruitment at age I is highly variable (e.g., Shallow Lake 1976-1985 average female age I recruitment = 1476, standard deviation = 1057.8, coefficient of variation of female age I recruitment = 71.7%). Consequently changes in the control lake's population density are related to changes in female recruitment.

DISCUSSION

Our comparative life stage analysis conclusively illustrates the importance of measuring age- and sex-specific processes in the population dynamics of benthic crustaceans such as crayfish. Thus, although crayfish in both lakes proved very resilient to perturbation and exhibited density-dependent population regulation, the intensity, form and phasing of the feedback mechanisms were very different within the two systems. Shallow Lake males regulate the recruitment of females and juvenile males through biotic feedbacks related to intraspecific size-class interactions. Sexually mature age II males adjust male and female mortality rates between the hatchling and juvenile life stages. Therefore recruitment is determined by juvenile mortality. This imposes a two year oscillating cycle between annual juvenile-to-mature male growth and female year-class strength, and ultimately cohort egg production (Fig. 7). The eventual outcome of these mortality/growth interactions between life stages express themselves as changes in production and/or biomass. Despite these interactions annual production remains relatively constant within each lake (Momot 1986). Apparently each lake has a finite carrying capacity which the populations nearly attain in each successive year (e.g., annual production of 6-9 $gm.m^{2}.^{-1}$). By reducing natural mortality, exploitation modifies the relationship between crayfish numbers and biomass in Dock Lake. Such a recruitment response must be related to some actual underlying biological mechanism.

Obviously the life stage at which the male reaches sexual maturity regulates the population, but how is the biotic feedback manifested? One plausible explanation may involve the basic agonistic behaviour pattern affecting aggression and dispersal among conspecifics. The dominance order of crayfish is size related (Bovbjerg 1953, 1956). From behavioural observations mature individual males dominate over females regardless of size (Bovbjerg 1956). Bovbjerg and Stephen (1974) showed agonistic behaviour in **O. virilis** increased proportionately until their density reached 39 $crayfish.m^{2}.^{-1}$ in aquaria. Dominance is proportional to carapace length and correlates with **O. virilis** chela length (Lunt 1967). We propose that large chelae are not only essential for reproductive activities as suggested by Stein (1976), but are also important in dominance behaviour, which modifies life stage growth/mortality through intraspecific interactions. Large male chelae size is important in both the promiscuous mating system (Berrill and Arsenault 1984) and in any chance meeting between individuals because aggressive encounters (i.e., the general agonistic behaviour pattern) are indistinguishable from copulatory behaviour (Mason 1970). In contrast females only exhibit passive resistance to larger males during the breeding season (Berrill and Arsenault 1984). If size dominance is important to population life history patterns/variations then males should have larger chelae than females irregardless of reproductive condition. In **O. virilis** form I/form II male chelae are 8-24% longer and 5-16% wider than females (cf. Fig. 1; Weagle and Ozburn 1970). Therefore similar sized **O. virilis** (in terms of CL) have differentially sized chelae (i.e., males always have larger chelae). Also the sexually dimorphic growth of Dockand Shallow Lake crayfish results in large males having larger chelae than females of corresponding ages. Size dominance significantly increases individual males fitness once maturity is reached (i.e., adaptive significance). Thus the relationship between the behaviour pattern as related to the dimorphic growth pattern and the reproductive cycle, is the causal mechanism which both regulates population density and drives the cycle.

Male dominance determines breeding success in the panmictic mating system. The assumption being that males successfully mate with more than one female. Larger **Orconectes rusticus** (Girard) males are capable of multiple copulations (Berrill and Arsenault 1984). The presence of juvenile male density-dependent mortality and differential juvenile male fishing mortality, skews the sex ratio to favour females at maturity in **O. virilis** populations. Since all sexually mature females become annually gravid this illustrates the need for multiple matings. Sufficient numbers of males must be present in the population to fertilize them all. Therefore mature male aggression enhances individual fitness, in terms of opportunities for mating. However anything that the individual male can do to decrease the abundance of other sexually mature males and their contribution to future generations also increases his own individual fitness.

An intense negative feedback mechanism produces a strong density-dependent hatchling mortality relationship in Shallow Lake. Recruitment is suppressed during the short time period from egg extrusion until the YOY become fully independent of the female. During this time period yearling **O. virilis** males (i.e., age I+) co-occur with mature females releasing young in the shallowest water <0.5 m (Morgan unpublished data; Momot 1967). Capelli (1980) reported similar distributions of **Orconectes propinquus** (Girard) males and females. He found inshore males to be cannibalistic on the large number of newly hatched young until they reach a critical vulnerable size >8 mm carapace length (Capelli 1980). We hypothesize that cannibalism by age I+ male crayfish on the eggs and newly hatched YOY of mature female crayfish may provide the possibility for a negative feedback mechanism regulating population growth. After winter dormancy, immature males require a high quality/quantity food item in order to obtain enough energy to moult into their reproductive form during the short growing-season. A suitable (preferable?) protein source annually concentrated in a thermal regime favourable for metabolic activities and growth processes may be in the form of YOY crayfish. Also possible is the suppression of normal YOY exploratory and foraging activity by the males resulting in high hatchling mortality in all but the most favourable habitats (i.e., related to growth/mortality interactions in the hatchling stage; Fig. 8). Adjustment of population growth potential through the bioenergetic needs of maturing males may thus constitute a biological basis for regulation especially when coupled to annual nutrient budgets prevalent at northern latitudes. The resultant is regulation of the annual production cycle as well as optimization of the brood stock biomass. Regulation of population growth, at the earliest and most abundant life stage, is accomplished by temporal and spatial juxtaposition of vulnerable egg-bearing females with behaviourally dominant males.

Exploitation weakens this density-dependent regulatory mechanism as females are less vulnerable than males to stationary fishing gear. Fishing inadvertently removes `excess' age I and age II males. At the same time, the selective gear protects the female stock as the population increases (Table 2 and Figure 6). The increase in the exploitation rate of male age groups increases hatchling survival and juvenile growth and survival. Interestingly enough, male and female egg-to-YOY mortality still exhibits density dependence at efforts reaching 4000 trap-days.

The variable hatching growth rate extends the critical period of YOY crayfish vulnerability to intraspecific aggression increasing the ability of mature males to enhance individual fitness through decreases in male juvenile density. The vulnerability of age I males to the trap fishery becomes a major determinant controlling the recruitment to the exploited population. Increased fishing effort results in higher fishing mortality during the age I-to-age II period of life. This in turn releases the self-regulating mechanism inhibiting hatchling survival and increases recruitment of crayfish at age I. Increasing levels of nominal effort up to 4000 trap-days does not impact the reproductive cycle since enough mature males survive to fertilize the females. At present mature Dock Lake males represent 10-20% of the exploitable stock. Exploitation thus results in increased population growth and population vigour in Dock Lake.

Thus behavioural, ecological and evolutionary viewpoints are integrated into our mature male regulating hypothesis. The advantages of male dominance within the juvenile life stages, although subtle, appear cumulative over time and result in a dynamic oscillatory coexistence between the sexes in natural populations (Fig. 7). The adult male life history strategy is fixed (since behaviours are unaltered by exploitation) and reduces the number of subadult males and generates an adult sex ratio biased towards females at high densities (Fig. 6). However among both sexes dominance affects resource allocation related to growth (Fig. 7) presumably in relation to quality of diet. Self-regulation strongly synchronizes this cycle so that female year-class frequency oscillates with a periodicity at twice the mean age of male sexual maturity. Under 'natural' conditions the effects of mortality/growth interactions regulates egg production. Therefore the dominance order maximizes reproduction even under adverse conditions. These density-dependent mechanisms, operating at the behavioural and physiological levels, give crayfish populations resilience and stability to environmental perturbations despite widely varying levels of annual exploitation.

The resulting management implications from this study of these self-regulating populations are significant and far-reaching for all crustacean fishery managers. Firstly extremely high levels of fishing effort have not collapsed the stock rather, counter-intuitively, exploitation encourages population increases. Perhaps management of crayfish and other trap fisheries for benthic crustaceans could be dictated by supply-demand economics provided harvest begins after the females reproduce. In such cases the optimal management strategy would be based on the economic value of harvesting the resource relative to the cost of employing stationary gear, bait and labour (i.e., a cost-effective fishery). This should protect the fishery from over-capitalization.

Secondly in the case of crayfish, the age- and sex-specific growth and mortality rates are predictable and if based on exploitation rates could provide reliable and accurate yield forecasts. The active intrinsic control manifested by these populations actually simplifies management. Climatic variation appears unimportant in population regulation, however any extreme significant seasonal weather departure from the basic regional climatic pattern could adversely affect local crayfish populations (i.e., limit ultimate population density). The growing season's thermal regime, related to the timing of spring warming, most likely limits life history characteristics related to temperature thresholds. These thresholds effect both fecundity and the growth process (ecdysis) by acting as a metabolic rate-controller (Aiken 1969a and b).

We believe sex/size regulations used to protect the breeding stock rather than protecting the stock would instead reinforce density-dependent YOY production and thus decrease juvenile recruitment. The goals of basing harvest stategies upon sex/size limits are the following: protect the populations reproductive potential by reducing adult fishing mortality, control fishing effort on the exploitable stock and, enhance juvenile survival and recruitment (Jamieson and Caddy 1986). The combination of a male only fishery and a specific size limit set above the size of sexual maturity would increase juvenile growth rates and instead decrease recruitment to the exploitable stock. In all likelihood this worse-case scenario would increase the amplitude in the cyclic oscillations between annual male juvenile-to-mature life stage growth and female year-class strength, thus destabilizing the system. This management situation/biological phenomenon is currently receiving considerable attention in the Dungeness Crab (**Cancer magister**) fisheries of the West Coast (Botsford 1986). If such a negative biotic feedback mechanism is common to other crustaceans, then management guidelines which seek to protect the breeding stock may in fact be detrimental.

Our third recommendation is that the forecasting of year-class strength in exploited and natural crayfish populations not be based on empirical indices of YOY abundance even if sampling techniques produce consistent and reliable estimates. In most crustacean populations quantitative sampling of this life stage is extremely difficult resulting in estimates of poor precision. In natural crayfish populations year-class strength is determined by female recruitment processes. Therefore it is unlikely that changes in population density can be detected using traditional relative abundance estimates (based on standardized male catch-per-unit effort indices) due to differential sex and size catchability (Momot 1967). In addition, male catch-per-unit effort indices would be measuring only those crayfish which survived from age I-to-age II (i.e., a measure of the variability in survival from the stable recruitment of male age I crayfish to sexual maturity) and as such would not be indicative of population abundance (in unexploited crayfish stocks). Future year-class strengths in Dock Lake can be calculated with precision based on the harvest rate of age I male crayfish. This index is easily estimated from changes in relative abundance or catch and effort data (Ricker 1975). More importantly the harvest data would provide **a priori** detection of recruitment overfishing (i.e., if the total annual harvest exceeds predicted age I recruitment to the exploitable stock). Recruitment is an index of the populations productivity (i.e., recruitment is the product of natality and survival rates) relative to perturbations. Effective management based on annual harvest and annual recruitment relationships should protect crayfish populations from overfishing and provide forecasts of the next year's potential recruitment and yield. Density-dependent mortality during the prerecruit phase buffers crayfish against external influences and dampens population variability in natural stocks, while protecting exploited stocks from recruitment failures due to fishing pressure. These key functional relationships determine potential limits of recruitment to the exploitable stock.

The multistage recruitment process is controlled by a stock-dependent component and a density-dependent function (Ware 1980). Initial reproductive effort, measured as YOY abundance, is stock-dependent upon the number of mature age II males in the population (i.e., reproductive effort is reduced as the stock of age II males increases). However actual year-class strength is determined from YOY-to-age I (prerecruit life stage) by a density-dependent mortality function related to male mortality during the maturing life stage. It is the age-specificity of this mortality which determines the adaptive population response.

The dependence of increased population growth, to sustain increased harvests, depends on high levels of exploitation of male crayfish approaching sexual maturity. The potential for sudden and unpredictable changes in population density could occur if exploitation rates on the age I male crayfish should decrease. In order to maintain the high population/high harvest relationship, exploitation must annually remove 70% of the age I males. Failure to harvest a sufficient proportion produces a one year lag in YOY production related to increased age II male density (Fig. 1). Weak year-classes would result from decreased age I recruitment to the exploitable stock two years after the low exploitation rate, regardless of the intervening harvest levels. This situation occurred during the 1984 harvest. Harvesting with 250 traps for 16 days significantly reduced age I male vulnerability (i.e., 57% exploitation rate) compared to similar nominal efforts in 1982 and 1983 (i.e., 4000 trap-days) using 200 traps for 20 days (i.e., age I male exploitation rates: 1982 = 70%; 1983 =71%). The induced time delay response resulted in poor YOY production in 1985, approximately 350-475% lower than average. The severe fishing effort of 6000 trap-days in 1985 harvested approximately as many crayfish as we predicted could be recruited to the stock at the maximum age I year-class strength. We predict a significant decline in the 1986 population density caused by pseudo-recruitment overfishing. However the ability to alter harvest rates related to nominal effort should protect the population from continued recruitment overfishing (i.e., provided that future removals take 70% of the age I males). This should increase hatchling survival (Fig. 1) and increase the net recruitment rate by age I (Fig. 4). The probability of overfishing increases as harvest rates approach recruitment rates. Paradoxically it appears that in order to maintain high yields from high density crayfish populations and to avoid the recruitment underfishing syndrome, requires increasing exploitation of newly recruited small male crayfish. Therefore our fourth recommendation is that crayfish stocks in northern climates could be managed using total allowable catch quotas with safety margins, relative to predicted age I male recruitment rates, to minimize the potential of future recruitment failures.

The resilience of northern crayfish populations to severe levels of fishing effort is the result of increased population vigour mediated through alterations in survival of prerecruit age-classes. The stability of the altered life-stage interactions becomes related to the exploitation level of maturing male crayfish. Our insights into crayfish population regulation suggest that the method of harvest must remove the maturing male life stage in order to compliment the stock-dependent mechanism. Inadvertently the size and sex selective exploitation stimulates the regulatory mechanism. This `tricks' the biotic feedback into higher population growth (i.e., the synergistic relationship perceives a low population density when in fact the population level is increasing). Resilience and stability of crayfish populations to perturbations is manifested through intrinsic regulation of early life history parameters which govern future population growth. Our research indicates the importance of considering size-based (and hence growth rate) life history patterns relative to the synchrony of life cycle events (both seasonally and annually). By considering these processes acting together, our deterministic model of crayfish dynamics has unified descriptive natural history with population ecology. We believe that the integrated responses between growth and mortality are controlled by the behavioural mechanism of size and sex dominance. From an evolutionary viewpoint, the synchronized and fixed timing of northern Orconectid crayfish life history phenomena evolved as a functional linkage between the seasonality of environmental conditions (which govern metabolic activity in poikilotherms) and an adaptive biological strategy (which regulates population growth through inter-/intra-life stage feedbacks and dominance behaviour).

Authors' Note: The 1986 Dock Lake crayfish population declined by 45% from 9273 in 1985 to 5109 due to poor recruitment of age I crayfish (number of age I recruits: male = 1176; female = 702). However 1986 YOY production increased to 6336 young (number of YOY: male = 2672; female = 3664). Exploitation rate of age I males in 1986 was 72%. Therefore the population density should increase to approximately 7000 crayfish in 1987.

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SUMMARY

Populations of the crayfish **Orconectes virilis** (Hagen) in northern climates exhibit strong density-dependent regulation. This results in remarkable stability and resilience to perturbation. Climatic variation, measured as changes in seasonal weather parameters, fail to influence life history characteristics in the exploited Dock Lake population. In this population, the juvenile female growth response supplants climatic and growth induced depression of fecundity and YOY production. In the control population in Shallow Lake, per capita fecundity is mediated through changes in growth potential while YOY production variation in turn relates to spring temperature regimes. Despite differences in per capita fecundity responses between lakes, total annual egg production (i.e., population fecundity) is similar. Therefore the reproductive response to exploitation has been through an adjustment in hatchling survival rates.

Removal of over one-third of the available stock (age I+) increased female growth during the life stage when sexual maturity is reached. Dock Lake's hatchling mortality rates decreased, but female juvenile and adult male mortality rates increased. These increases in life stage mortality rates occur during the developmental period when sexual maturity is reached. Maturity appears to be an intrinsically fixed linear function of length. Alterations of growth and mortality rates therefore determine **when?** and **how many?** individuals reproduce. However the ability of the exploited population to withstand severe levels of fishing effort is the result of interactions between the behavioural mechanism governing dominance and a biotic feedback which alters juvenile survival.

The higher population growth potential in Dock Lake is caused by enhanced juvenile recruitment (from YOY-to-age I) resulting from increased fishing of age I males. YOY production rises until available habitat becomes limiting. The result is that Dock Lake annually produces between 7000-9500 YOY irregardless of fecundity constraints. Year-class strength is determined by over-winter natural mortality of YOY. With higher exploitative pressure, fishing mortality of age I male crayfish increased. This produced an approximate 50:50 sex ratio regardless of the density of the exploitable stock.

Although the unexploited population in Shallow Lake is also regulated by a similar maturing male life stage mechanism, the result depresses recruitment of juvenile life stages. The male intraspecific competition/aggression restricts survival between the hatchling and juvenile life stages. Though YOY production becomes extremely variable in Shallow Lake, differential juvenile mortality controls recruitment of males and females. Age I male recruitment becomes constrained within a restricted range of approximately 1000-1300 crayfish. Changes in Shallow Lake population density result from changes in female recruitment. Thus at high population densities, Shallow Lake's adult population exhibits a female biased sex ratio. The outcome of these growth/mortality interactions is that maturing male growth exhibits a cyclic covariation with female year-class strength and cohort egg production.

The number of crayfish harvested using passive fishing gear is influenced by changes in: sampling intensity, sampling duration and behavioural responses. These relationships affect age- and sex-specific catchabilities. Male catchability stabilizes at a gear density of 200 minnow traps until sampling duration exceeds 20 days. Female catchability decreases with increasing sampling intensity and sampling duration. At high nominal efforts behavioural responses related to removal of dominant age II males increases the proportion of small crayfish in the catch. The percentage of the exploitable stock harvested is related to a nominal effort of up to 4000 trap-days. However harvests using this stationary gear fail to remove more than 75% of the males, 50% of the females, or combined 60% of the exploitable stock. This protects crayfish stocks from over-exploitation at high nominal efforts.

The intrinsic responses of these crayfish to human disturbance and natural, stochastic, environmental variation imparts numerical population stability related to life history characteristics. Annual losses of 60-70% of age I and older crayfish is balanced by juvenile recruitment. Over-exploitation using modified minnow traps appears unlikely regardless of nominal effort.

APPENDIX

Appendix A.

Example of multiple regression analysis of Dock and Shallow Lake YOY density-dependent relationships.

LEGEND of combined alphanumeric codes (raw data followed by statistics)

YEAR = calemdar year
GDD = growing-degree-days >15oC
IIM = density of age II male crayfish
SL = Shallow Lake
DL = Dock Lake
YOY = density of young-of-year
M = male
F = female
G = instantaneous growth rate egg-to-YOY
Z = instantaneous mortality rate egg-to-YOY

```
         YEAR          GDD          IIMSL        YOYMSL       YOYFSL        IIMDL
  1     76.000       188.20       225.00       7427.0       5190.0       268.00
  2     77.000       116.60       292.00       5845.0       6350.0       383.00
  3     78.000       116.30       400.00       4770.0       4620.0       796.00
  4     79.000       135.80       551.00       2033.0       1748.0       469.00
  5     80.000       154.90       699.00       1500.0       2075.0       336.00
  6     81.000       170.00       981.00       2500.0       1292.0       469.00
  7     82.000       85.900       646.00       2454.0       2139.0       371.00
  8     83.000       254.60       790.00       1215.0       1222.0       475.00
  9     84.000       168.80       989.00       2268.0       4225.0       693.00
 10     85.000       114.20       1215.0       365.00       502.00       970.00
        YOYMDL       YOYFDL         GMSL         ZMSL         GFSL         ZFSL
  1     5634.0       4711.0       1.7400       1.9500       1.7000       2.3100
  2     4224.0       2907.0       1.6300       2.2100       1.6300       2.1300
  3     3513.0       4455.0       1.4600       3.6100       1.4800       3.6400
  4     3719.0       6273.0       1.3000       4.2200       1.2800       4.3700
  5     2750.0       2392.0       1.3400       4.3000       1.3100       3.9700
  6     3300.0       3300.0       1.4100       3.6600       1.3600       4.3200
  7     3175.0       4383.0       1.2100       4.6000       1.1800       4.7300
  8     3868.0       3631.0       1.1900       5.1000       1.1500       5.0900
  9     4396.0       5351.0       1.2600       4.5100       1.2500       3.8900
 10     745.00       796.00       1.2000       5.5800       1.1600       5.2600
          GMDL         ZMDL         GFDL         ZFDL
  1     1.6000       2.7800       1.5400       2.9600
  2     1.6600       2.4200       1.5700       2.8000
  3     1.1500       3.7600       1.1100       3.5200
  4     1.2700       3.3600       1.2200       2.9200
  5     1.3700       3.0700       1.2700       3.2100
  6     1.4100       3.2400       1.3500       3.2400
  7     1.1700       3.3400       1.1300       3.0200
  8     1.1400       3.5300       1.0800       3.5900
  9     1.2000       3.7400       1.1500       3.5400
 10     1.2200       4.2100       1.2100       4.6000
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        2.686E+04    3.906E+03         6.88       0.0002
LNIIMSL        -3.741E+03    600.4            -6.23       0.0004
GDD             7.183E-01    6.863             0.10       0.9196

CASES INCLUDED           10       MISSING CASES    0
DEGREES OF FREEDOM        7
OVERALL F             19.50       P VALUE      0.0009
ADJUSTED R SQUARED   0.8043
R SQUARED            0.8478
MEAN SQUARED ERROR    9.830E+05
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        2.694E+04    3.595E+03         7.49       0.0001
LNIIMSL        -3.735E+03    560.1            -6.67       0.0002

CASES INCLUDED           10       MISSING CASES    0
DEGREES OF FREEDOM        8
OVERALL F             44.48       P VALUE      0.0000
ADJUSTED R SQUARED   0.8285
R SQUARED            0.8476
MEAN SQUARED ERROR    8.615E+05
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT        2.141E+04    5.423E+03         3.95        0.0055
LNIIMSL        -2.816E+03    833.6            -3.38        0.0118
GDD            -3.084        9.529            -0.32        0.7557

CASES INCLUDED            10       MISSING CASES     0
DEGREES OF FREEDOM         7
OVERALL F              5.890       P VALUE      0.0250
ADJUSTED R SQUARED    0.5208
R SQUARED             0.6273
MEAN SQUARED ERROR     1.895E+06


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT        2.109E+04    5.025E+03         4.20        0.0030
LNIIMSL        -2.838E+03    782.8            -3.63        0.0067

CASES INCLUDED            10       MISSING CASES     0
DEGREES OF FREEDOM         8
OVERALL F              13.15       P VALUE      0.0030
ADJUSTED R SQUARED    0.5744
R SQUARED             0.6217
MEAN SQUARED ERROR     1.683E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------   ------
CONSTANT       1.241E+04   6.046E+03        2.05      0.0793
LNIIMDL       -1.622E+03   919.9           -1.76      0.1212
GDD            7.680       7.694            1.00      0.3514

CASES INCLUDED          10       MISSING CASES    0
DEGREES OF FREEDOM       7
OVERALL F            2.529       P VALUE      0.1408
ADJUSTED R SQUARED  0.2536
R SQUARED           0.4195
MEAN SQUARED ERROR   1.190E+06


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------   ------
CONSTANT       1.475E+04   5.573E+03        2.65      0.0294
LNIIMDL       -1.813E+03   899.6           -2.02      0.0786

CASES INCLUDED          10       MISSING CASES    0
DEGREES OF FREEDOM       8
OVERALL F            4.064       P VALUE      0.0606
ADJUSTED R SQUARED  0.2540
R SQUARED           0.3368
MEAN SQUARED ERROR   1.190E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        8.392E+03    9.616E+03         0.87       0.4118
LNIIMDL        -789.4        1.463E+03        -0.54       0.6062
GDD             2.056        12.24             0.17       0.8713

CASES INCLUDED            10        MISSING CASES    0
DEGREES OF FREEDOM         7
OVERALL F              1.866E-01    P VALUE       0.9022
ADJUSTED R SQUARED -0.2206
R SQUARED             0.0506
MEAN SQUARED ERROR   3.011E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        9.017E+03    8.310E+03         1.09       0.3095
LNIIMDL        -840.5        1.341E+03        -0.63       0.5484

CASES INCLUDED            10        MISSING CASES    0
DEGREES OF FREEDOM         8
OVERALL F              3.927E-01    P VALUE       0.6876
ADJUSTED R SQUARED -0.0724
R SQUARED             0.0468
MEAN SQUARED ERROR   2.645E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     -----
CONSTANT        5.318E+03    891.9               5.96      0.0003
IIMDL          -3.414        1.579              -2.16      0.0626

CASES INCLUDED           10        MISSING CASES     0
DEGREES OF FREEDOM        8
OVERALL F             4.673        P VALUE       0.0452
ADJUSTED R SQUARED   0.2898
R SQUARED            0.3687
MEAN SQUARED ERROR    1.132E+06


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     -----
CONSTANT        4.893E+03    1.335E+03           3.67      0.0063
IIMDL          -2.051        2.363              -0.87      0.4107

CASES INCLUDED           10        MISSING CASES     0
DEGREES OF FREEDOM        8
OVERALL F             7.532E-01    P VALUE       0.5015
ADJUSTED R SQUARED  -0.0282
R SQUARED            0.0861
MEAN SQUARED ERROR    2.536E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GMSL

PREDICTOR
VARIABLES     COEFFICIENT   STD ERROR    STUDENT'S T      P
----------    -----------   ---------    -----------   ------
CONSTANT         1.637      1.729E-01       9.46       0.0000
IIMSL         -4.439E-04    1.443E-04      -3.08       0.0179
GDD            2.567E-04    9.642E-04       0.27       0.7977

CASES INCLUDED          10      MISSING CASES    0
DEGREES OF FREEDOM       7
OVERALL F            4.732      P VALUE      0.0415
ADJUSTED R SQUARED  0.4533
R SQUARED           0.5748
MEAN SQUARED ERROR   1.937E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GMSL

PREDICTOR
VARIABLES     COEFFICIENT   STD ERROR    STUDENT'S T      P
----------    -----------   ---------    -----------   ------
CONSTANT         1.673      1.006E-01      16.63       0.0000
IIMSL         -4.402E-04    1.350E-04      -3.26       0.0115

CASES INCLUDED          10      MISSING CASES    0
DEGREES OF FREEDOM       8
OVERALL F            10.63      P VALUE      0.0056
ADJUSTED R SQUARED  0.5168
R SQUARED           0.5705
MEAN SQUARED ERROR   1.712E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZMSL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR     STUDENT'S T      P
---------    -----------   ---------     -----------   ------
CONSTANT       2.163       9.689E-01        2.23       0.0607
IIMSL          2.908E-03   8.085E-04        3.60       0.0088
GDD           -1.083E-03   5.403E-03       -0.20       0.8468

CASES INCLUDED          10       MISSING CASES    0
DEGREES OF FREEDOM       7
OVERALL F            6.477       P VALUE     0.0198
ADJUSTED R SQUARED  0.5490
R SQUARED           0.6492
MEAN SQUARED ERROR   6.080E-01


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZMSL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR     STUDENT'S T      P
---------    -----------   ---------     -----------   ------
CONSTANT       2.011       5.623E-01        3.58       0.0072
IIMSL          2.892E-03   7.551E-04        3.83       0.0050

CASES INCLUDED          10       MISSING CASES    0
DEGREES OF FREEDOM       8
OVERALL F            14.67       P VALUE     0.0021
ADJUSTED R SQUARED  0.6031
R SQUARED           0.6472
MEAN SQUARED ERROR   5.351E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
---------     -----------    ---------    -----------    ------
CONSTANT        1.657        1.702E-01        9.74       0.0000
IIMSL         -4.719E-04     1.420E-04       -3.32       0.0127
GDD            8.631E-05     9.489E-04        0.09       0.9301

CASES INCLUDED          10        MISSING CASES     0
DEGREES OF FREEDOM       7
OVERALL F            5.548        P VALUE      0.0288
ADJUSTED R SQUARED  0.5026
R SQUARED           0.6132
MEAN SQUARED ERROR   1.876E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
---------     -----------    ---------    -----------    ------
CONSTANT        1.670        9.854E-02       16.94       0.0000
IIMSL         -4.707E-04     1.323E-04       -3.56       0.0074

CASES INCLUDED          10        MISSING CASES     0
DEGREES OF FREEDOM       8
OVERALL F            12.66        P VALUE      0.0033
ADJUSTED R SQUARED  0.5643
R SQUARED           0.6127
MEAN SQUARED ERROR   1.643E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        2.268        9.403E-01         2.41       0.0467
IIMSL           2.536E-03    7.847E-04         3.23       0.0144
GDD            -1.195E-04    5.243E-03        -0.02       0.9824

CASES INCLUDED           10       MISSING CASES     0
DEGREES OF FREEDOM        7
OVERALL F             5.262       P VALUE      0.0326
ADJUSTED R SQUARED   0.4864
R SQUARED            0.6005
MEAN SQUARED ERROR    5.727E-01


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        1.670        9.854E-02        16.94       0.0000
IIMSL          -4.707E-04    1.323E-04        -3.56       0.0074

CASES INCLUDED           10       MISSING CASES     0
DEGREES OF FREEDOM        8
OVERALL F             12.66       P VALUE      0.0033
ADJUSTED R SQUARED   0.5643
R SQUARED            0.6127
MEAN SQUARED ERROR    1.643E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GMDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T        P
---------     -----------    ---------     -----------     ------
CONSTANT        1.660        2.635E-01         6.30        0.0004
IIMDL        -4.926E-04      2.658E-04        -1.85        0.1063
GDD          -5.555E-04      1.236E-03        -0.45        0.6666

CASES INCLUDED            10        MISSING CASES     0
DEGREES OF FREEDOM         7
OVERALL F              1.717        P VALUE      0.2500
ADJUSTED R SQUARED    0.1374
R SQUARED             0.3291
MEAN SQUARED ERROR     3.022E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GMDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T        P
---------     -----------    ---------     -----------     ------
CONSTANT        1.562        1.382E-01        11.30        0.0000
IIMDL        -4.638E-04      2.448E-04        -1.89        0.0947

CASES INCLUDED            10        MISSING CASES     0
DEGREES OF FREEDOM         8
OVERALL F              3.590        P VALUE      0.0771
ADJUSTED R SQUARED    0.2235
R SQUARED             0.3097
MEAN SQUARED ERROR     2.720E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T       P
---------    -----------   ---------    -----------    ------
CONSTANT       2.016       4.342E-01        4.64       0.0024
IIMDL          2.047E-03   4.380E-04        4.67       0.0023
GDD            1.715E-03   2.036E-03        0.84       0.4274

CASES INCLUDED            10        MISSING CASES     0
DEGREES OF FREEDOM         7
OVERALL F              10.96        P VALUE      0.0049
ADJUSTED R SQUARED    0.6888
R SQUARED             0.7579
MEAN SQUARED ERROR     8.205E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T       P
---------    -----------   ---------    -----------    ------
CONSTANT       2.321       2.357E-01        9.85       0.0000
IIMDL          1.957E-03   4.173E-04        4.69       0.0016

CASES INCLUDED            10        MISSING CASES     0
DEGREES OF FREEDOM         8
OVERALL F              22.00        P VALUE      0.0006
ADJUSTED R SQUARED    0.7000
R SQUARED             0.7334
MEAN SQUARED ERROR     7.907E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
---------     -----------    ---------    -----------    ------
CONSTANT        1.570        2.546E-01        6.16       0.0005
IIMDL         -4.123E-04     2.569E-04       -1.61       0.1525
GDD           -6.041E-04     1.194E-03       -0.51       0.6284

CASES INCLUDED             10        MISSING CASES     0
DEGREES OF FREEDOM          7
OVERALL F               1.296        P VALUE      0.3487
ADJUSTED R SQUARED     0.0617
R SQUARED              0.2702
MEAN SQUARED ERROR    2.821E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
---------     -----------    ---------    -----------    ------
CONSTANT        1.462        1.341E-01       10.91       0.0000
IIMDL         -3.809E-04     2.374E-04       -1.60       0.1472

CASES INCLUDED             10        MISSING CASES     0
DEGREES OF FREEDOM          8
OVERALL F               2.575        P VALUE      0.1370
ADJUSTED R SQUARED     0.1489
R SQUARED              0.2435
MEAN SQUARED ERROR    2.559E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
----------    -----------    ----------   -----------    ------
CONSTANT        1.816        4.074E-01        4.46       0.0029
IIMDL           2.139E-03    4.110E-04        5.20       0.0012
GDD             2.690E-03    1.910E-03        1.41       0.2020

CASES INCLUDED            10       MISSING CASES     0
DEGREES OF FREEDOM         7
OVERALL F              13.55       P VALUE      0.0027
ADJUSTED R SQUARED    0.7361
R SQUARED             0.7948
MEAN SQUARED ERROR     7.225E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
----------    -----------    ----------   -----------    ------
CONSTANT        2.294        2.387E-01        9.61       0.0000
IIMDL           1.999E-03    4.227E-04        4.73       0.0015

CASES INCLUDED            10       MISSING CASES     0
DEGREES OF FREEDOM         8
OVERALL F              22.38       P VALUE      0.0005
ADJUSTED R SQUARED    0.7037
R SQUARED             0.7367
MEAN SQUARED ERROR     8.112E-02
```

Appendix B.

Example of multiple regression analysis of Dock and Shallow Lake life stage inter-relationships.

LEGEND of combined alphanumeric codes (raw data followed by regressions)

YOY = density of young-of-year
M = male
F = female
DL = Dock Lake
SL = Shallow Lake
G = instantaneous growth rate
Z = instantaneous mortality rate
EO = egg-to-YOY life stage
OI = YOY-to-age I life stage
ITOII = age I-to-age II life stage
GDD = growing-degree-days >15oC

```
9     8485.0         168.80              M           365.00         502.00         9.9000E-01
      YOYMDL         YOYFDL         GEOMSL          ZEOMSL         GEOFSL         ZEOFSL
1     4224.0         2907.0         1.6300          2.2100         1.6300         2.1300
2     3513.0         4455.0         1.4600          3.6100         1.4800         3.6400
3     3719.0         6273.0         1.3000          4.2200         1.2800         4.3700
4     2750.0         2392.0         1.3400          4.3000         1.3100         3.9700
5     3300.0         3300.0         1.4100          3.6600         1.3600         4.3200
6     3175.0         4383.0         1.2100          4.6000         1.1800         4.7300
7     3868.0         3631.0         1.1900          5.1000         1.1500         5.0900
8     4396.0         5351.0         1.2600          4.5100         1.2500         3.8900
9     745.00         796.00              M               M              M              M
      GEOMDL         ZEOMDL         GEOFDL          ZEOFDL         GOIMSL         ZOIMSL
1     1.6600         2.4200         1.5700          2.8000         4.9000E-01     2.0700
2     1.1500         3.7600         1.1100          3.5200         5.6000E-01     1.5900
3     1.2700         3.3600         1.2200          2.9200         7.1000E-01     1.3700
4     1.3700         3.0700         1.2700          3.2100         9.6000E-01     4.1000E-01
5     1.4100         3.2400         1.3500          3.2400         8.5000E-01     6.3000E-01
6     1.1700         3.3400         1.1300          3.0200         8.3000E-01     1.0800
7     1.1400         3.5300         1.0800          3.5900         9.9000E-01     6.8000E-01
8     1.2000         3.7400         1.1500          3.5400         1.0300              M
9          M              M              M               M         8.8000E-01     4.1000E-01
      GOIFSL         ZOIFSL         GOIMDL          ZOIMDL         GOIFDL         ZOIFDL
1     3.9000E-01     2.3100         6.1000E-01      1.7700         5.9000E-01     1.6000
2     4.7000E-01     1.5500         5.3000E-01      1.2100         5.2000E-01     6.6000E-01
3     6.1000E-01     1.6500         9.7000E-01      1.3200         9.7000E-01     1.4800
4     9.1000E-01     1.2000E-01     9.5000E-01      1.3800         9.3000E-01     1.8900
5     8.5000E-01     3.3000E-01     8.4000E-01      1.4800         8.9000E-01     9.2000E-01
6     7.4000E-01     2.3000E-01     8.1000E-01      6.9000E-01     7.8000E-01     8.1000E-01
7     9.1000E-01     1.2000E-01     1.0100          2.8000E-01     1.0100         4.7000E-01
8     9.4000E-01          M         1.0600          3.9000E-01     1.0200         5.2000E-01
9     8.6000E-01          M         9.3000E-01      2.6000E-01     9.0000E-01     4.4000E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT        175.5        1.274E+03         0.14        0.8958
ZMITOIISL       3.078E+03    901.1             3.42        0.0189
GDD             6.348        7.379             0.86        0.4289

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        5
OVERALL F             6.263        P VALUE      0.0380
ADJUSTED R SQUARED   0.6006
R SQUARED            0.7147
MEAN SQUARED ERROR    1.052E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT        1.137E+03    597.0             1.91        0.1054
ZMITOIISL       3.093E+03    881.3             3.51        0.0127

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        6
OVERALL F             12.32        P VALUE      0.0075
ADJUSTED R SQUARED   0.6179
R SQUARED            0.6725
MEAN SQUARED ERROR    1.006E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT       -1.398E+03    1.350E+03        -1.04        0.3478
ZMITOIISL       3.101E+03    955.1             3.25        0.0228
GDD             17.46        7.821             2.23        0.0760

CASES INCLUDED             8        MISSING CASES     1
DEGREES OF FREEDOM         5
OVERALL F              7.901        P VALUE       0.0241
ADJUSTED R SQUARED    0.6635
R SQUARED             0.7596
MEAN SQUARED ERROR    1.182E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT        1.247E+03    834.5             1.49        0.1857
ZMITOIISL       3.141E+03    1.232E+03         2.55        0.0435

CASES INCLUDED             8        MISSING CASES     1
DEGREES OF FREEDOM         6
OVERALL F              6.502        P VALUE       0.0315
ADJUSTED R SQUARED    0.4401
R SQUARED             0.5201
MEAN SQUARED ERROR    1.966E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ----------   -----------   ------
CONSTANT       3.085E+03   1.663E+03        1.85      0.1131
ZMITOIIDL     -258.0       1.221E+03       -0.21      0.8397
GDD            2.741       8.932            0.31      0.7693

CASES INCLUDED           9       MISSING CASES    0
DEGREES OF FREEDOM       6
OVERALL F            6.315E-02   P VALUE     0.9774
ADJUSTED R SQUARED -0.3058
R SQUARED           0.0206
MEAN SQUARED ERROR   1.542E+06


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ----------   -----------   ------
CONSTANT       2.907E+03   1.332E+03        2.18      0.0655
GDD            2.538       8.252            0.31      0.7674

CASES INCLUDED           9       MISSING CASES    0
DEGREES OF FREEDOM       7
OVERALL F            9.458E-02   P VALUE     0.9109
ADJUSTED R SQUARED -0.1276
R SQUARED           0.0133
MEAN SQUARED ERROR   1.331E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
---------     -----------    ---------    -----------     ------
CONSTANT        3.639E+03    2.525E+03        1.44        0.1995
ZMITOIIDL       6.687        1.854E+03        0.00        0.9973
GDD             4.918E-01    13.56            0.04        0.9722

CASES INCLUDED             9       MISSING CASES     0
DEGREES OF FREEDOM         6
OVERALL F            6.864E-04     P VALUE      1.0000
ADJUSTED R SQUARED -0.3330
R SQUARED           0.0002
MEAN SQUARED ERROR   3.552E+06


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON YOYFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
---------     -----------    ---------    -----------     ------
CONSTANT        3.644E+03    2.015E+03        1.81        0.1134
GDD             4.970E-01    12.48            0.04        0.9693

CASES INCLUDED             9       MISSING CASES     0
DEGREES OF FREEDOM         7
OVERALL F            1.586E-03     P VALUE      0.9984
ADJUSTED R SQUARED -0.1426
R SQUARED           0.0002
MEAN SQUARED ERROR   3.045E+06
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOMSL

PREDICTOR
VARIABLES      COEFFICIENT    STD ERROR     STUDENT'S T       P
---------      -----------    ---------     -----------     -----
CONSTANT        1.137         9.880E-02        11.51        0.0001
ZMITOIISL       2.989E-01     6.990E-02         4.28        0.0079
GDD             3.256E-04     5.723E-04         0.57        0.5940

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        5
OVERALL F             9.354        P VALUE        0.0171
ADJUSTED R SQUARED   0.7047
R SQUARED            0.7891
MEAN SQUARED ERROR    6.327E-03


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOMSL

PREDICTOR
VARIABLES      COEFFICIENT    STD ERROR     STUDENT'S T       P
---------      -----------    ---------     -----------     -----
CONSTANT        1.187         4.460E-02        26.61        0.0000
ZMITOIISL       2.996E-01     6.583E-02         4.55        0.0039

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        6
OVERALL F             20.72        P VALUE        0.0020
ADJUSTED R SQUARED   0.7380
R SQUARED            0.7754
MEAN SQUARED ERROR    5.614E-03
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
----------    -----------    ----------    -----------    ------
CONSTANT        5.550        5.504E-01        10.08       0.0002
ZMITOIISL      -1.794        3.893E-01        -4.61       0.0058
GDD            -3.575E-03    3.188E-03        -1.12       0.3131

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        5
OVERALL F             11.34        P VALUE      0.0114
ADJUSTED R SQUARED   0.7471
R SQUARED            0.8194
MEAN SQUARED ERROR    1.963E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
----------    -----------    ----------    -----------    ------
CONSTANT        5.008        2.693E-01        18.60       0.0000
ZMITOIISL      -1.802        3.975E-01        -4.53       0.0040

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        6
OVERALL F             20.54        P VALUE      0.0021
ADJUSTED R SQUARED   0.7363
R SQUARED            0.7740
MEAN SQUARED ERROR    2.048E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOFSL

PREDICTOR
VARIABLES    COEFFICIENT    STD ERROR    STUDENT'S T      P
---------    -----------    ---------    -----------    ------
CONSTANT       1.087        9.577E-02       11.35       0.0001
ZMITOIISL      3.334E-01    6.775E-02        4.92       0.0044
GDD            4.005E-04    5.547E-04        0.72       0.5026

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        5
OVERALL F             12.44        P VALUE      0.0094
ADJUSTED R SQUARED   0.7657
R SQUARED            0.8326
MEAN SQUARED ERROR    5.944E-03
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOFSL

PREDICTOR
VARIABLES    COEFFICIENT    STD ERROR    STUDENT'S T      P
---------    -----------    ---------    -----------    ------
CONSTANT       1.148        4.402E-02       26.07       0.0000
ZMITOIISL      3.343E-01    6.498E-02        5.14       0.0021

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        6
OVERALL F             26.47        P VALUE      0.0011
ADJUSTED R SQUARED   0.7844
R SQUARED            0.8152
MEAN SQUARED ERROR    5.470E-03
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        6.039        3.670E-01        16.45       0.0000
ZMITOIISL      -1.798        2.596E-01        -6.93       0.0010
GDD            -6.814E-03    2.126E-03        -3.21       0.0238

CASES INCLUDED              8         MISSING CASES     1
DEGREES OF FREEDOM          5
OVERALL F               29.56         P VALUE      0.0013
ADJUSTED R SQUARED     0.8908
R SQUARED              0.9220
MEAN SQUARED ERROR      8.729E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        5.006        2.806E-01        17.84       0.0000
ZMITOIISL      -1.814        4.142E-01        -4.38       0.0047

CASES INCLUDED              8         MISSING CASES     1
DEGREES OF FREEDOM          6
OVERALL F               19.19         P VALUE      0.0025
ADJUSTED R SQUARED     0.7221
R SQUARED              0.7618
MEAN SQUARED ERROR      2.222E-01


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    ------
CONSTANT        5.101        1.014             5.03       0.0024
GDD            -7.092E-03    6.316E-03        -1.12       0.3044

CASES INCLUDED              8         MISSING CASES     1
DEGREES OF FREEDOM          6
OVERALL F               1.261         P VALUE      0.3490
ADJUSTED R SQUARED     0.0359
R SQUARED              0.1737
MEAN SQUARED ERROR      7.709E-01
```

```
          SPEARMAN RANK CORRELATIONS, CORRECTED FOR TIES

            RYCMDL    RYCMSL     RGMDL     RGMSL    RYCFDL    RYCFSL     RGFDL
RYCMDL      1.0000
RYCMSL      0.0714    1.0000
RGMDL       0.4018    0.2589    1.0000
RGMSL       0.3125    0.1696    0.7857    1.0000
RYCFDL      0.6696    0.4196   -0.0714   -0.0357    1.0000
RYCFSL     -0.4196    0.6518   -0.3929   -0.1786    0.3214    1.0000
RGFDL       0.4196    0.1339    0.6429    0.8929    0.2857   -0.0357    1.0000
RGFSL      -0.0089    0.6696    0.2857    0.5357    0.2857    0.6429    0.5714
GDDYC       0.0804   -0.3482   -0.4286   -0.2143   -0.2143   -0.3214   -0.4286
GDDALL     -0.2946   -0.7411   -0.0714    0.2500   -0.5714   -0.3214    0.2143

             RGFSL     GDDYC    GDDALL
RGFSL       1.0000
GDDYC      -0.4286    1.0000
GDDALL     -0.0714    0.1786    1.0000

 DEGREES OF FREEDOM            5

MAX. DIFF. ALLOWED BETWEEN TIES      1.00000E-5

 CASES INCLUDED                7      MISSING CASES     0
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------    -----
CONSTANT       1.246       2.653E-01       4.70        0.0054
ZMITOIIDL    -1.170E-01    1.970E-01      -0.59        0.5783
GDD           9.348E-04    1.424E-03       0.66        0.5406

CASES INCLUDED             8        MISSING CASES    1
DEGREES OF FREEDOM         5
OVERALL F            3.598E-01      P VALUE      0.7852
ADJUSTED R SQUARED -0.2239
R SQUARED           0.1258
MEAN SQUARED ERROR   3.888E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------    -----
CONSTANT       1.165       2.150E-01       5.42        0.0016
GDD           8.589E-04    1.340E-03       0.64        0.5452

CASES INCLUDED             8        MISSING CASES    1
DEGREES OF FREEDOM         6
OVERALL F            4.110E-01      P VALUE      0.6803
ADJUSTED R SQUARED -0.0919
R SQUARED           0.0641
MEAN SQUARED ERROR   3.469E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOMDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------    -----
CONSTANT       1.380       1.617E-01       8.53        0.0001
ZMITOIIDL    -1.054E-01    1.867E-01      -0.56        0.5926

CASES INCLUDED             8        MISSING CASES    1
DEGREES OF FREEDOM         6
OVERALL F            3.191E-01      P VALUE      0.7384
ADJUSTED R SQUARED -0.1078
R SQUARED           0.0505
MEAN SQUARED ERROR   3.519E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOMDL

PREDICTOR
VARIABLES      COEFFICIENT    STD ERROR     STUDENT'S T       P
----------     -----------    ----------    -----------    ------
CONSTANT         3.247        6.608E-01         4.91       0.0044
ZMITOIIDL        2.713E-01    4.908E-01         0.55       0.6042
GDD             -1.010E-03    3.548E-03        -0.28       0.7873

CASES INCLUDED              8        MISSING CASES      1
DEGREES OF FREEDOM          5
OVERALL F               1.807E-01    P VALUE        0.9051
ADJUSTED R SQUARED -0.3056
R SQUARED             0.0674
MEAN SQUARED ERROR    2.413E-01


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOMDL

PREDICTOR
VARIABLES      COEFFICIENT    STD ERROR     STUDENT'S T       P
----------     -----------    ----------    -----------    ------
CONSTANT         3.103        3.896E-01         7.96       0.0002
ZMITOIIDL        2.588E-01    4.498E-01         0.58       0.5859

CASES INCLUDED              8        MISSING CASES      1
DEGREES OF FREEDOM          6
OVERALL F               3.311E-01    P VALUE        0.7305
ADJUSTED R SQUARED -0.1057
R SQUARED             0.0523
MEAN SQUARED ERROR    2.043E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
----------    -----------    ---------    -----------    ------
CONSTANT        1.192        2.365E-01        5.04       0.0040
ZMITOIIDL     -1.270E-01     1.757E-01       -0.72       0.5023
GDD            9.356E-04     1.270E-03        0.74       0.4944

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        5
OVERALL F             4.887E-01    P VALUE       0.7051
ADJUSTED R SQUARED -0.1711
R SQUARED           0.1635
MEAN SQUARED ERROR   3.092E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
----------    -----------    ---------    -----------    ------
CONSTANT        1.105        1.948E-01        5.67       0.0013
GDD            8.533E-04     1.213E-03        0.70       0.5083

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        6
OVERALL F             4.944E-01    P VALUE       0.6328
ADJUSTED R SQUARED -0.0778
R SQUARED           0.0761
MEAN SQUARED ERROR   2.846E-02


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GEOFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
----------    -----------    ---------    -----------    ------
CONSTANT        1.326        1.457E-01        9.10       0.0001
ZMITOIIDL     -1.153E-01     1.682E-01       -0.69       0.5184

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        6
OVERALL F             4.705E-01    P VALUE       0.6459
ADJUSTED R SQUARED -0.0818
R SQUARED           0.0727
MEAN SQUARED ERROR   2.856E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
---------     -----------    ---------    -----------    ------
CONSTANT        3.139        4.535E-01        6.92       0.0010
ZMITOIIDL       2.481E-01    3.368E-01        0.74       0.4944
GDD            -6.878E-04    2.435E-03       -0.28       0.7889

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        5
OVERALL F             2.949E-01    P VALUE       0.8281
ADJUSTED R SQUARED  -0.2523
R SQUARED            0.1055
MEAN SQUARED ERROR    1.137E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZEOFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T      P
---------     -----------    ---------    -----------    ------
CONSTANT        3.041        2.674E-01       11.37       0.0000
ZMITOIIDL       2.396E-01    3.087E-01        0.78       0.4671

CASES INCLUDED            8        MISSING CASES     1
DEGREES OF FREEDOM        6
OVERALL F             6.025E-01    P VALUE       0.5775
ADJUSTED R SQUARED  -0.0602
R SQUARED            0.0913
MEAN SQUARED ERROR    9.624E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIMSL

PREDICTOR
VARIABLES     COEFFICIENT   STD ERROR    STUDENT'S T      P
---------     -----------   ---------    -----------    ------
CONSTANT        9.402E-01   1.331E-01        7.06       0.0009
ZMITOIISL      -4.098E-01   9.419E-02       -4.35       0.0074
GDD             5.603E-04   7.712E-04        0.73       0.5001

CASES INCLUDED              8       MISSING CASES    1
DEGREES OF FREEDOM          5
OVERALL F               9.674       P VALUE       0.0160
ADJUSTED R SQUARED     0.7125
R SQUARED              0.7947
MEAN SQUARED ERROR      1.149E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIMSL

PREDICTOR
VARIABLES     COEFFICIENT   STD ERROR    STUDENT'S T      P
---------     -----------   ---------    -----------    ------
CONSTANT        1.025       6.124E-02       16.74       0.0000
ZMITOIISL      -4.085E-01   9.039E-02       -4.52       0.0040

CASES INCLUDED              8       MISSING CASES    1
DEGREES OF FREEDOM          6
OVERALL F               20.43       P VALUE       0.0021
ADJUSTED R SQUARED     0.7351
R SQUARED              0.7730
MEAN SQUARED ERROR      1.059E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT        4.020E-01    6.831E-01         0.59        0.5878
ZMITOIISL       1.084        4.201E-01         2.58        0.0614
GDD             5.578E-04    5.283E-03         0.11        0.9210

CASES INCLUDED             7        MISSING CASES    2
DEGREES OF FREEDOM         4
OVERALL F              4.193        P VALUE       0.0999
ADJUSTED R SQUARED    0.5156
R SQUARED             0.6771
MEAN SQUARED ERROR     1.716E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIMSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     ------
CONSTANT        4.681E-01    2.453E-01         1.91        0.1147
ZMITOIISL       1.103        3.412E-01         3.23        0.0232

CASES INCLUDED             7        MISSING CASES    2
DEGREES OF FREEDOM         5
OVERALL F              10.44        P VALUE       0.0164
ADJUSTED R SQUARED    0.6114
R SQUARED             0.6762
MEAN SQUARED ERROR     1.377E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    -----
CONSTANT        8.884E-01    1.470E-01         6.04       0.0018
ZMITOIISL      -4.369E-01    1.040E-01        -4.20       0.0085
GDD             5.051E-04    8.517E-04         0.59       0.5789

CASES INCLUDED              8         MISSING CASES     1
DEGREES OF FREEDOM          5
OVERALL F               8.952         P VALUE       0.0187
ADJUSTED R SQUARED     0.6944
R SQUARED              0.7817
MEAN SQUARED ERROR      1.401E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T      P
---------     -----------    ---------     -----------    -----
CONSTANT        9.650E-01    6.654E-02        14.50       0.0000
ZMITOIISL      -4.357E-01    9.822E-02        -4.44       0.0044

CASES INCLUDED              8         MISSING CASES     1
DEGREES OF FREEDOM          6
OVERALL F               19.68         P VALUE       0.0023
ADJUSTED R SQUARED     0.7274
R SQUARED              0.7663
MEAN SQUARED ERROR      1.250E-02
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     -----
CONSTANT        2.305E-01    6.657E-01         0.35        0.7466
ZMITOIISL       2.016        4.094E-01         4.92        0.0079
GDD            -3.752E-03    5.148E-03        -0.73        0.5065

CASES INCLUDED            7         MISSING CASES     2
DEGREES OF FREEDOM        4
OVERALL F             13.23         P VALUE      0.0152
ADJUSTED R SQUARED   0.8030
R SQUARED            0.8687
MEAN SQUARED ERROR    1.629E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIFSL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
---------     -----------    ---------     -----------     -----
CONSTANT       -2.140E-01    2.541E-01        -0.84        0.4381
ZMITOIISL       1.891        3.534E-01         5.35        0.0031

CASES INCLUDED            7         MISSING CASES     2
DEGREES OF FREEDOM        5
OVERALL F             28.61         P VALUE      0.0018
ADJUSTED R SQUARED   0.8215
R SQUARED            0.8513
MEAN SQUARED ERROR    1.477E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIMDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
---------     -----------    ---------    -----------    ------
CONSTANT        4.595E-01    7.433E-02        6.18       0.0008
ZMITOIIDL       4.818E-01    5.458E-02        8.83       0.0001
GDD             3.782E-05    3.991E-04        0.09       0.9276

CASES INCLUDED              9       MISSING CASES     0
DEGREES OF FREEDOM          6
OVERALL F               39.52       P VALUE      0.0002
ADJUSTED R SQUARED     0.9059
R SQUARED              0.9294
MEAN SQUARED ERROR    3.078E-03


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIMDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
---------     -----------    ---------    -----------    ------
CONSTANT        4.649E-01    4.428E-02       10.50       0.0000
ZMITOIIDL       4.824E-01    5.027E-02        9.60       0.0000

CASES INCLUDED              9       MISSING CASES     0
DEGREES OF FREEDOM          7
OVERALL F               92.07       P VALUE      0.0000
ADJUSTED R SQUARED     0.9192
R SQUARED              0.9293
MEAN SQUARED ERROR    2.643E-03
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIMDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
---------     -----------    ---------    -----------    ------
CONSTANT        1.791        7.422E-01        2.41       0.0523
ZMITOIIDL     -8.580E-01     5.450E-01       -1.57       0.1664
GDD           -7.671E-04     3.985E-03       -0.19       0.8537

CASES INCLUDED            9        MISSING CASES     0
DEGREES OF FREEDOM        6
OVERALL F             1.306        P VALUE      0.3561
ADJUSTED R SQUARED   0.0710
R SQUARED            0.3033
MEAN SQUARED ERROR    3.069E-01


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIMDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR    STUDENT'S T       P
---------     -----------    ---------    -----------    ------
CONSTANT        1.682        4.432E-01        3.79       0.0068
ZMITOIIDL     -8.693E-01     5.032E-01       -1.73       0.1277

CASES INCLUDED            9        MISSING CASES     0
DEGREES OF FREEDOM        7
OVERALL F             2.985        P VALUE      0.1155
ADJUSTED R SQUARED   0.1988
R SQUARED            0.2989
MEAN SQUARED ERROR    2.647E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
----------    -----------    ----------    ------------    ------
CONSTANT        4.911E-01    8.988E-02         5.46        0.0016
ZMITOIIDL       4.749E-01    6.600E-02         7.20        0.0004
GDD            -2.018E-04    4.826E-04        -0.42        0.6904

CASES INCLUDED              9        MISSING CASES     0
DEGREES OF FREEDOM          6
OVERALL F               25.95        P VALUE      0.0008
ADJUSTED R SQUARED     0.8618
R SQUARED              0.8964
MEAN SQUARED ERROR    4.502E-03


UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON GOIFDL

PREDICTOR
VARIABLES     COEFFICIENT    STD ERROR     STUDENT'S T       P
----------    -----------    ----------    ------------    ------
CONSTANT        4.623E-01    5.428E-02         8.52        0.0001
ZMITOIIDL       4.719E-01    6.163E-02         7.66        0.0001

CASES INCLUDED              9        MISSING CASES     0
DEGREES OF FREEDOM          7
OVERALL F               58.63        P VALUE      0.0000
ADJUSTED R SQUARED     0.8781
R SQUARED              0.8933
MEAN SQUARED ERROR    3.971E-03
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIFDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------   ------
CONSTANT       1.276       8.305E-01        1.54      0.1754
ZMITOIIDL    -1.522E-01    6.098E-01       -0.25      0.8113
GDD          -1.135E-03    4.459E-03       -0.25      0.8076

CASES INCLUDED           9       MISSING CASES    0
DEGREES OF FREEDOM       6
OVERALL F            7.118E-02   P VALUE     0.9733
ADJUSTED R SQUARED -0.3024
R SQUARED           0.0232
MEAN SQUARED ERROR   3.843E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIFDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------   ------
CONSTANT       1.171       6.661E-01        1.76      0.1223
GDD          -1.255E-03    4.126E-03       -0.30      0.7699

CASES INCLUDED           9       MISSING CASES    0
DEGREES OF FREEDOM       7
OVERALL F            9.250E-02   P VALUE     0.9127
ADJUSTED R SQUARED -0.1280
R SQUARED           0.0130
MEAN SQUARED ERROR   3.328E-01
```

```
UNWEIGHTED LEAST SQUARES LINEAR REGRESSION ON ZOIFDL

PREDICTOR
VARIABLES    COEFFICIENT   STD ERROR    STUDENT'S T      P
---------    -----------   ---------    -----------   ------
CONSTANT       1.114       4.971E-01        2.24      0.0600
ZMITOIIDL    -1.688E-01    5.643E-01       -0.30      0.7735

CASES INCLUDED           9       MISSING CASES    0
DEGREES OF FREEDOM       7
OVERALL F            8.952E-02   P VALUE     0.9154
ADJUSTED R SQUARED -0.1284
R SQUARED           0.0126
MEAN SQUARED ERROR   3.330E-01
```

Appendix C.

Example of correlation analysis of relative rates and temperature.

LEGEND (raw data followed by correlation matrix)

YEAR = calendar year
RYCMDL = relative year-class strength Dock Lake males
RYCMSL = relative year-class strength Shallow Lake males
RYCFDL = relative year-class strength Dock Lake females
RYCFSL = relative year-class strength Shallow Lake females
RGMDL = relative growth Dock Lake males
RGMSL = relative growth Shallow Lake males
RGFDL = relative growth Dock Lake females
RGFSL = relative growth Shallow Lake females
GDDYC = growing-degree-days >15oC at hatching (first growing season)
GDDALL = growing-degree-days >15oC through entire life cycle (sum of four successive growing seasons)

```
         YEAR          RYCMDL         RYCMSL          RGMDL          RGMSL          RYCFDL
 1      76.000         1.1000         1.0000         7.9000E-01     7.2000E-01     1.1000
 2      77.000         9.7000E-01     1.0400         8.0000E-01     7.9000E-01     1.0000
 3      78.000         9.9000E-01     1.0300         1.1900         1.1000         9.1000E-01
 4      79.000         1.1600         1.2300         1.1700         1.4900         1.1500
 5      80.000         7.2000E-01     1.0100         7.7000E-01     8.8000E-01     9.4000E-01
 6      81.000         9.9000E-01     8.9000E-01     1.1000         1.3900         9.0000E-01
 7      82.000         1.0100         1.0000         1.0100         9.0000E-01     1.1400
        RYCFSL          RGFDL          RGFSL          GDDYC          GDDALL
 1      7.8000E-01     7.8000E-01     5.9000E-01     188.20         556.90
 2      1.1200         7.9000E-01     8.7000E-01     116.60         523.60
 3      8.1000E-01     9.6000E-01     9.4000E-01     116.30         577.00
 4      1.1100         1.4000         1.4800         135.80         546.60
 5      1.5000         9.4000E-01     1.0100         154.90         665.40
 6      7.3000E-01     1.0000         8.5000E-01     170.00         679.30
 7      1.0300         1.2600         8.8000E-01     85.900         623.50
```