

AN EVALUATION OF  
THE CURRENT MINIMUM LEGAL SIZE LIMIT  
FOR THE DUNGENESS CRAB (Cancer magister DANA) FISHERY  
NEAR TOFINO, BRITISH COLUMBIA

By

BARRY DOUGLAS SMITH

B.Sc., The University of New Brunswick, 1974  
M.Sc., The University of British Columbia, 1979

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES  
(Department of Zoology)

We accept this thesis as conforming  
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

November 1988

© Barry Douglas Smith, 1988

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of

Zoology

The University of British Columbia  
1956 Main Mall  
Vancouver, Canada  
V6T 1Y3

Date

5 August 88

## ABSTRACT

The Dungeness crab (Cancer magister Dana) trap fishery in British Columbia has been regulated by a minimum legal size limit of 165 mm spine-to-spine carapace width (CW, 154 mm notch-to-notch CW) since early this century. Evaluation of the size limit by yield- and eggs-per-recruit analyses has been precluded by a lack of information on basic population variables such as growth, mortality, movement and mating behavior. Information on these variables was obtained in an intensive two year study of the Dungeness crab fishery near Tofino, B.C. from April 1985 until March 1987. A cohort of pre-recruit males and females was followed as the males entered the fishery and were subsequently exploited, yielding information on moult increments-at-size, length of intermoult periods, size-at-maturity, size of mating pairs, mortality, movement, commercial fishing success and exploitation rates.

Male C. magister entered the fishery during their fourth year after settlement. Size frequency analysis revealed that nearly all legal-sized (>154 mm notch-to-notch CW) males are within the  $155.0 \pm 11.2$  mm instar ( $\approx 50\%$  of this instar). Sublegal-sized males in this instar have a high annual natural mortality rate ( $M=2.8-4.5$ ), hence a low probability (<10%) of surviving to legal size. Legal-sized males have a high annual fishing mortality rate ( $F=5.1-6.9$ ). Consequently, a small component of the commercial catch is composed of males in larger instars.

Despite females not being landed, the negative slope of female catch curves from four regional fisheries was steepest for the most heavily fished region and shallowest for the most lightly fished region. Females mate after moulting while accompanied by a larger male, and in a heavily fished population larger males may be absent. Thus, the catch curves suggested the possibility of reduced mating and moulting, and consequently fewer large females, in heavily fished populations.

Yield-per-recruit analysis suggests landings might be markedly improved by lowering the minimum legal size limit. However, eggs-per-recruit analysis, which modeled the possible consequences of removing large males, suggests that for a heavily fished population the current size limit may result in up to a 50% decline in population egg production relative to an unfished population. The historical presumption that the current minimum legal size limit for males does not impact on population egg production should be reconsidered.

To facilitate calibration of trap samples biased by differences in soak times, parameters for models describing changes in bait effectiveness over time, and agonistic interactions between crabs within a trap and those attempting to enter that trap, were estimated. Parameter estimates were obtained by simulating the entry and exit of crabs into and out of traps based on experiments which (1) emphasized the above two processes, and (2) estimated the daily probabilities of crabs of different sizes escaping traps.

## Table of Contents

Abstract.....	ii
List of Tables.....	vi
List of Figures.....	ix
Acknowledgments.....	xv
1 INTRODUCTION.....	1
2 DESCRIPTION OF STUDY AREAS.....	6
3 FIELD METHODS.....	13
3.1 MORPHOMETRICS.....	13
3.2 BEAM TRAWL SAMPLING.....	15
3.3 TRAP SAMPLING.....	16
3.4 FEMALE SIZE-AT-MATURITY.....	16
3.5 MATING PAIRS.....	17
3.6 TRAP DISTRIBUTION.....	17
3.7 TRAP PERFORMANCE EXPERIMENTS.....	18
3.7.1 TRAP TYPES.....	20
3.7.2 CATCH RATES OF TRAPS IN GRIDS.....	21
3.7.3 ESCAPE OF CRABS FROM TRAPS.....	21
3.7.4 SOAK TIME EXPERIMENT.....	22
3.7.5 BAIT-EFFECTIVENESS EXPERIMENT.....	23
3.8 MARK-RECOVERY PROGRAM.....	24
4 RESULTS.....	27
4.1 SPECIES COLLECTED.....	27
4.2 MORPHOMETRICS.....	27
4.3 FEMALE SIZE-AT-MATURITY.....	28
4.4 MATING PAIRS.....	30
4.5 MOULT INCREMENTS.....	32

4.6	GROWTH.....	36
4.7	TRAP PERFORMANCE EXPERIMENTS.....	43
4.7.1	CATCH RATES OF TRAPS IN GRIDS.....	43
4.7.2	ESCAPE OF CRABS FROM TRAPS.....	44
4.7.3	SOAK TIME AND BAIT EFFECTS.....	50
4.8	TRAP DISTRIBUTION.....	68
4.9	COMMERCIAL EXPLOITATION OF MALES.....	70
4.10	MALE MATING ACTIVITY.....	78
4.11	SPATIAL AND TEMPORAL DISTRIBUTIONS.....	84
4.12	TAG RETENTION AND TAG INDUCED MORTALITY.....	95
4.13	FISHING AND NATURAL MORTALITY OF MALES.....	96
4.14	FISHING INTENSITY AND FEMALE CATCH CURVES IN SELECTED FISHERIES.....	107
5	YIELD- AND EGGS-PER-RECRUIT MODEL.....	111
5.1	DEVELOPMENT.....	111
5.2	RESULTS.....	117
6	DISCUSSION.....	123
6.1	TRAP PERFORMANCE EXPERIMENTS.....	123
6.2	SPATIAL AND TEMPORAL DISTRIBUTIONS.....	128
6.3	GROWTH AND MORTALITY.....	131
6.4	YIELD- AND EGGS-PER-RECRUIT.....	137
6.5	SUMMARY.....	148
7	LITERATURE CITED.....	153

## List of Tables

Table 4.5.1. Linear regression models for male <u>C. magister</u> moult increments-at-size for four data sets collected from British Columbia (B.C.) and California (Cal.).	33
Table 4.5.2. Linear regression models for female <u>C. magister</u> moult increments-at-size for three data sets collected from British Columbia (B.C.) and California (Cal.).	33
Table 4.6.1. Mean and standard deviations (SD, sd) for carapace widths defining instars of male <u>C. magister</u> >80 mm CW.	40
Table 4.6.2. Mean and standard deviations (SD, sd) for carapace widths defining instars of female <u>C. magister</u> >80 mm CW.	40
Table 4.6.3. The relative proportions of male <u>C. magister</u> >80 mm CW within consecutive instars for a time series of beam trawl samples. The value for each date includes all males captured within two weeks of that date. The dominant instar is highlighted by an asterisk.	41
Table 4.6.4. The relative proportions of female <u>C. magister</u> >80 mm CW within consecutive instars for a time series of beam trawl samples. The value for each date includes all females captured within two weeks of that date. The dominant instar is highlighted by an asterisk.	42
Table 4.7.1.1. Comparison of the mean number of <u>C. magister</u> caught per trap for 16 perimeter versus nine interior traps in two 5 by 5 grids, and between all traps in each grid.	43
Table 4.7.2.1. The relative retention of crabs <155 mm CW, for Traps C-D, and crabs <145 mm CW, for Trap B, relative to Trap A. The relative retention for a trap type is the number of crabs caught by that trap type divided by the number caught by Trap A after equivalent one day soaks. For Trap A n=536 for crabs <155 mm CW, and n=322 for crabs <145 mm CW.	47
Table 4.7.2.2. The probabilities of male <u>C. magister</u> being retained by Traps A-D for 24 h.	47

Table 4.7.3.1. Comparison of different models explaining densities and size frequency distributions of <u>C. magister</u> in sets of traps which experienced different soak times and bait ages during equivalent experiments in 1985 and 1986. The objective function (A) is the separation statistic of Schnute and Fournier (1980). P is the number of parameters in the model. AIC (see text) measures model performance, the lower the value the more suitable the model.	57
Table 4.10.1. The percent of male <u>C. magister</u> , tagged when soft-shelled, which were hard-shelled when recovered. The results are reported for 30 day intervals of time-at-large. The carapace widths of recovered males were approximately normally distributed ( $153.4 \pm 6.0$ mm) and ranged from 135-173 mm.	80
Table 4.11.1. Abundance of female <u>C. magister</u> >145 mm CW in commercial traps in May and June of 1985 and 1986.	88
Table 4.11.2. Densities of two to three year old ( $\approx 75$ -145 mm CW) <u>C. magister</u> from beam trawl samples near Indian Island.	88
Table 4.11.3. Summary of tag recoveries, by location, of sublegal- and legal-sized male <u>C. magister</u> between April 1985 and August 1986. The number of trap hauls was determined by interviewing fishermen. Only records from fishermen whose effort was known are reported. Except where noted, recoveries were from within the study area as defined in Fig. 2.1 (page 9).	89
Table 4.11.4. Summary of tag recoveries, by location, of female <u>C. magister</u> between April 1985 and August 1986. The number of trap hauls was determined by interviewing fishermen. Only records from fishermen whose effort was known are reported. All recoveries were from within the study area as defined in Fig. 2.1 (page 9).	90
Table 4.13.1. Statistics of the linear relationship in Fig. 4.13.1 from which the annual instantaneous rate of disappearance of sublegal-sized (145-155 mm CW) male <u>C. magister</u> was estimated. The relationship has the form $Y = a + b \cdot X$ ; where Y is the logarithm of the number of recoveries within consecutive one month intervals, and X is the time-at-large in days.	97



Table 4.13.2. Statistics of the quadratic relationship in Fig. 4.13.1 which suggests the mortality rate may increase as the time-at-large for sublegal-sized (145-155 mm CW) male <u>C. magister</u> increases. The relationship has the form $Y = a + b \cdot X + c \cdot X^2$ ; where Y is the logarithm of the number of recoveries within consecutive one month intervals, and X is the time-at-large in days.	97
Table 4.13.3. Statistics of the linear relationship in Fig. 4.13.2 from which the annual instantaneous rate of disappearance (Z) of legal-sized male <u>C. magister</u> was estimated. The relationship has the form $Y = a + b \cdot X$ ; where Y is the logarithm of the number of recoveries within consecutive 15 day intervals, and X is the time-at-large in days.	98
Table 4.13.4. Statistics of the linear relationship in Fig. 4.13.4 estimating the mean time-at-large for recovered tagged sublegal-sized male <u>C. magister</u> . The relationship has the form $Y = a + b \cdot X$ ; where Y is the time to recovery (in days), and X is the pre-moult carapace width.	99
Table 4.13.5. Summary of survivorship to legal size of male <u>C. magister</u> which were tagged when sublegal size, and recovered when legal size, for 5 mm intervals from 125-155 mm CW.	102
Table 4.14.1. Comparisons among different measures of fishing effort, and fishing impact, on male <u>C. magister</u> populations in four regional fisheries defined by Statistical Area (SA). The statistical areas do not differ markedly in area. Annual statistics include the metric tonnes landed (t) and the number of days fishing (DF).	109
Table 5.1.1. The mean and standard deviation (mm) of normally distributed male and female <u>C. magister</u> instars for the age and time of year when they are nearly fully formed. Males become sexually active in the 155.0 mm instar.	112

## List of Figures

- Figure 2.1. Map of the main study area near Tofino, British Columbia. The stippled areas are intertidal mudflats. The dashed lines delimit the main study area. Selected sites are referenced by capital letters. The arrow indicates the main channel out to sea. Insert I locates the Dixon Entrance fishery (a). Insert II locates the main study area, the Holberg Inlet fishery (a), and the Fraser delta fishery (b).  
.....9
- Figure 2.2. Time series of the annual tonnage of C. magister landed in the Statistical Area 1, 24 and 29 fisheries.  
.....10
- Figure 2.3. Time series of the annual number of days fishing for C. magister in the Statistical Area 1, 24 and 29 fisheries.  
.....11
- Figure 2.4. Time series of the annual number of vessels which reported landings of C. magister from the Statistical Area 24 fishery near Tofino, B.C.  
.....12
- Figure 3.7.1. Layout of trap grids designed to emphasize the effects of different soak times (A), changes in bait effectiveness (B), and trap selectivity (C), on the density and size frequency distribution of C. magister. For (A) and (B) soak time (in days) is encircled, for (C) trap type is encircled.  
.....19
- Figure 4.3.1. The percent of female C. magister inseminated as a function of carapace width.  
.....29
- Figure 4.4.1. Carapace widths of C. magister mating pairs. The lines (Eqns. 4.4.1 and 2) define the apparent limits in carapace widths required for a mating embrace. Circles represent data from Butler (unpub. data), squares represent data from this study.  
.....31
- Figure 4.5.1. Male C. magister moult increments as a function of pre-moult carapace width. The plot uses data from British Columbia and California. Data from this study are represented by squares.  
.....34

Figure 4.5.2. Female <u>C. magister</u> moult increments as a function of pre-moult carapace width. The plot uses data from British Columbia and California. Data from this study are represented by squares.	35
Figure 4.6.1. Size frequency distributions for all male and female <u>C. magister</u> collected in beam trawl samples from June 1985 until September 1986.	37
Figure 4.7.2.1. The percent of male <u>C. magister</u> retained by Trap A for 24 h, as a function of carapace width.	48
Figure 4.7.2.2. Size frequency distributions of <u>C. magister</u> caught in Traps A-D. Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.	49
Figure 4.7.3.1. Comparison of size frequency distributions of <u>C. magister</u> in traps soaked 24 h in the soak time (ST, 20 traps) and bait effectiveness (BE, 16 traps) experiments in 1985 and 1986. Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.	61
Figure 4.7.3.2. Size frequency distributions of <u>C. magister</u> for sets of 20 type A traps with different soak times from equivalent experiments in 1985 and 1986. Solid circles profile predicted size frequency distributions using Model '4' (Table 4.7.3.1). Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.	62
Figure 4.7.3.3. The relative rate at which <u>C. magister</u> enter Trap A, as a function of the ratio between the weight of crabs in a trap, and the weight of the crab attempting to enter the trap. This plot uses the best parameter estimates for Eqn. 4.7.3.3 from Model '4' (Table 4.7.3.1).	63
Figure 4.7.3.4. The relative entry rate of <u>C. magister</u> into Trap A as a function of bait age. This plot uses the best parameter estimates for Eqn. 4.7.3.5 from Model '4' (Table 4.7.3.1).	64

- Figure 4.7.3.5. Response surface of the predicted changes in the size frequency distribution of C. magister within 20 type A traps, as a function of time. These results use the best parameter estimates for Eqns. 4.7.3.3 and 5 from Model '4' (Table 4.7.3.1). Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.  
.....65
- Figure 4.7.3.6. Response surface of the predicted size frequency distributions of C. magister within 10 sets of 16 type A traps. Each set used bait ranging in age from zero to eight days, soaked for one day. The bait was removed for the ninth day. The vertical lines show the observed data for a particular combination of bait age and carapace width, for differences greater than one. These results use the best parameter estimates for Eqns. 4.7.3.3 and 5 from Model '4' (Table 4.7.3.1). Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.  
.....66
- Figure 4.7.3.7. The percent of soft-shelled legal-sized male C. magister in Trap A, as a function of soak time. These results were obtained from the soak time experiment performed near Indian Island (H; Fig. 2.1, page 9) in 1986. Above the S.D. bars is the number of legal-sized males caught in 20 traps.  
.....67
- Figure 4.8.1. (A) Time series comparison of the number of trap buoys counted in Lemmens Inlet, and the number of traps estimated by interviewing fishermen. (B) Time series of the number of traps estimated by interviewing fishermen. The 'Elsewhere' category includes traps fished outside the study area in Statistical Area 24 by fishermen who also fish in the study area. The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).  
.....69
- Figure 4.9.1. Diagram explaining how the degree of exploitation of male C. magister in the  $155.0 \pm 11.2$  mm instar was estimated. The proportion exploited ( $A/[A+B]$ ) was determined by size frequency analysis.  
.....73
- Figure 4.9.2. The percent of legal-sized male C. magister removed from the 155.0 mm instar by fishing, as determined by size frequency analysis of trap samples. The encircled data points are for upper Lemmens Inlet. The remainder are for the rest of the study area.  
.....74

Figure 4.9.3. Linear regression of virtual entry rates of male <u>C. magister</u> 145-155 mm CW into traps over time. Data from upper Lemmens Inlet, a poor crab habitat, are not included in this plot.	75
Figure 4.9.4. Time series of commercial catch rates of legal-sized male <u>C. magister</u> . The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).	76
Figure 4.9.5. Virtual entry rates of legal-sized male <u>C. magister</u> into traps over time. Data from upper Lemmens Inlet, a poor crab habitat, are not included in this plot.	77
Figure 4.10.1. The percent of male <u>C. magister</u> with mating marks (Butler 1960) as a function of carapace width. The minimum legal size limit is $\approx 154$ mm CW.	81
Figure 4.10.2. Time series of the percent of hard-shelled legal-sized ( $>154$ mm CW) male, legal-sized male with mating marks (Butler 1960), and sublegal-sized (140-154 mm CW) male <u>C. magister</u> with mating marks. Except where noted, all sample sizes are $>100$ crabs.	82
Figure 4.10.3. Time series indicating that the relative level of mating activity by legal-sized male <u>C. magister</u> in 1986 was $\approx 29\%$ of the level in 1985. The sublegal:legal mating ratio is obtained by dividing the percent of legal-sized males with mating marks by the percent of sublegal-sized males with mating marks. The ratio for May 1986 was excluded from the comparison for reasons given in the text.	83
Figure 4.11.1. Time series of densities for one year old ( $\approx 40$ -75 mm CW) male and female <u>C. magister</u> in the entrance to Lemmens Inlet (A), and on the shallow sand bottom of an exposed shore (B). Time series of densities of two to three year old ( $\approx 75$ -145 mm CW) male and female <u>C. magister</u> in the main channel out to sea (C). The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).	91
Figure 4.11.2. Time series of densities for two to three year old ( $\approx 75$ -145 mm CW) male and female <u>C. magister</u> in Lemmens Inlet. The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).	92

Figure 4.11.3. Time series comparison of two indices of abundance for female <u>C. magister</u> (>145 mm CW) in the study area, but excluding Lemmens Inlet, Browning Passage, and near Indian Island, where female densities were generally low (Table 4.11.1). 'Virtual entry rates' were estimated as in Section 4.9.	93
Figure 4.11.4. Frequency distributions of mean daily movement rates for male and female <u>C. magister</u> . Crabs were recovered after a mean of $\approx 150$ days-at-large.	94
Figure 4.13.1. Linear and quadratic regressions of recoveries over time for tagged male <u>C. magister</u> released and recovered as sublegal-sized crabs 145-155 mm CW. Most tagging was done from May-July 1985. The open circles were not included in the regression analyses because fishermen were not well prepared for the mark-recovery program at this time.	103
Figure 4.13.2. Linear regression of recoveries over time for 341 tagged male <u>C. magister</u> released and recovered as legal-sized crabs, mostly in spring 1986.	104
Figure 4.13.3. (A) Frequency distribution of release dates of sublegal-sized male <u>C. magister</u> . (B) Frequency distribution of recovery dates for those crabs released in (A) and recovered as legal-sized crabs.	105
Figure 4.13.4. Linear regression of time-at-large for male <u>C. magister</u> , tagged and released when sublegal size and recovered when legal size, on pre-moult carapace width.	106
Figure 4.14.1. Comparison of catch curves (Ricker 1975) for females from four regional <u>C. magister</u> fisheries defined by Statistical Area in British Columbia.	110
Figure 5.2.1. Relative egg production by <u>C. magister</u> populations as a function of the F:M mating ratio, and for three estimates of M. These results are not noticeably sensitive to the annual rate of decrease in egg production by females who fail to mate and moult in previous years.	120
Figure 5.2.2. Yield-per-recruit (YPR) for increasing fishing mortality (F). The results are reported relative to $F=\infty$ .	121

Figure 5.2.3. Yield-per-recruit is reported relative to 1.0 at 165 mm CW (S-S). Eggs-per-recruit are reported relative to an unfished population. The breadth of the relationships indicate the range when the annual decrease in egg production by females that did not mate and moult in previous years is varied from 0.0-1.0 times the egg production of the previous year. Both notch-to-notch (N-N) and spine-to-spine (S-S) carapace widths, and the current Canadian (C) and American (A) legal sizes, are noted.  
.....122

## ACKNOWLEDGMENTS

This study benefited from the initiative, supervision and support of Dr. Glen S. Jamieson, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia. I extend my thanks to him for providing this opportunity and for ensuring that the work proceeded with minimum uncertainty and pursuit of dead ends, and few missed opportunities. My research committee, headed by Dr. C.C. Lindsey of the Department of Zoology, University of British Columbia, provided encouragement during this study, and I thank them.

The skill and wisdom of the technical staff at the Pacific Biological Station ensured a productive, effective and enjoyable field program. I especially thank Messrs. Wolfgang Carolsfeld, Wayne Harling, Dwight Heritage, Antan Phillips and their student assistants for assuring efficient, and above all, safe field work. I admire and envy their skills.

My greatest appreciation is for the participation of the fishermen, which was essential for successful completion of this work. In particular, Messrs. Danny Barr, Ken Barr, Joe Barton, John Fraser, Barry Grumbach, Jamie Sloman and Peter White invited me to sample their catch on board their vessels from time to time. Messrs. Danny Barr, Ken Barr, John Fraser, Barry Grumbach and Leigh Hilbert not only retained tags from legal-sized crabs which they caught, but recorded all encounters of tagged crabs. Messrs. Mike Daniels, Alex Erickson,



John Fraser, Barry Grumbach, Dave Rae-Arthur, Jamie Sloman, Ralph Tielman and Leigh Hilbert provided precise post-moult measurements of tagged crabs, or retained legal-sized crabs so I could measure them later. Many other fishermen returned tags or retained them for collection later. Mr. Andre Turpin of Tri-Star Seafood Supply Limited, Vancouver, B.C. collected and returned tags from crabs purchased by his employer.

I thank Mr. Doug Swift, Department of Fisheries and Oceans, Tofino, B.C. for providing storage space for research equipment and for helping with this work in other ways.

I am very grateful to Mr. Terry H. Butler for permitting me to use unpublished data he collected in Dixon Entrance during the 1950's.

During this study I was supported by a graduate scholarship from the Canadian Department of Fisheries and Oceans. All data are their property and are maintained at the Pacific Biological Station, Nanaimo, British Columbia.

## 1 INTRODUCTION

The Dungeness crab (Cancer magister Dana) is fished commercially from Alaska to central California along the Pacific coast of North America. In American waters only males greater than 171 mm (6.75 in) carapace width (CW), measured from tip to tip of the tenth anterolateral spines, can be retained legally. In British Columbia, the minimum legal size limit is 165 mm CW. Both males and females can be retained, but in practice females are rarely retained because (1) few reach legal size, (2) fishermen believe it is poor conservation policy, and (3) the market is familiar only with males.

The Dungeness crab fishery is one of the most valuable invertebrate fisheries in British Columbia (\$5.15 million landed value in 1986) yet there has been little research attention since the 1950's, partly because C. magister represents only 1% of the landed value of sea products in British Columbia (Jamieson 1985). Additionally, British Columbia C. magister fisheries have had few perceived problems requiring scientific intervention, due in part to an  $\approx 40\%$  annual turnover of fishermen, and no core group of fishermen to lobby for attention (Jamieson 1985, 1986).

With the exception of a precipitous, and as yet unexplained, decline in C. magister landings along the east coast of the Queen Charlotte Islands about 1970 (Jamieson 1985, 1986), there appear to be no outstanding trends or patterns in the landing statistics for major regional fisheries in British Columbia. In contrast,

C. magister landings from California, Oregon, and Washington have shown coherent cyclical fluctuations with a periodicity of 9-10 years since at least the early 1950's, apparently reflecting male abundance (Botsford 1986a). It is not known whether cycles are nonexistent in British Columbia fisheries, or the landing statistics do not reflect abundance.

Because of their apparently predictable cyclic pattern and high value (Barry 1985, Demory 1985, Warner 1985, Methot 1986), American Dungeness crab fisheries have attracted much scientific attention. Several mechanisms have been proposed as causes of these cycles. Those involving density-dependent recruitment were among the first evaluated, and included: (1) reduced female fecundity due to an egg-predator worm (Wickham 1979), (2) cannibalism of adults on juveniles (Botsford and Wickham 1978), and (3) density-dependence in early life history (McKelvey et al. 1980).

A predator-prey hypothesis, with fishermen as the predator, has been rejected as an explanation of the cycles (Botsford et al. 1983). Salmon predation on crab larvae (Botsford et al. 1982, Thomas 1985), also seems unlikely to have caused the cycles. Recent research is focusing on the hypothesis that the cycles may have been caused by a cyclical pattern in wind stress, possibly in conjunction with density-dependent processes (Johnson et al. 1986, Botsford 1986b).

There have been no yield- or eggs-per-recruit analyses of the minimum legal size limit for C. magister because reliable estimates of growth and mortality have not been available (Methot 1986). A lack of information on growth and mortality was acknowledged as a limitation in most of the models proposed to explain the cyclic pattern of landings. Accurate estimates of population parameters are often difficult to acquire because of the logistic problems of performing experiments and sampling on an unbounded, exposed coast.

The purpose of this study was to estimate the vital statistics of growth, mortality, moulting, movement and reproduction for a relatively closed C. magister population in order to evaluate the current minimum legal size limit for C. magister. The current size limit of 165 mm spine-to-spine CW ( $\approx$ 154 mm notch-to-notch CW) has been in place in British Columbia since at least early this century, but there is no documentation of how this size was chosen (Jamieson 1985). With information from this study (supplemented by information from Hankin et al. (1985) on female growth, survivorship, and fecundity) yield- and eggs-per-recruit were analyzed to evaluate the assumption that the current minimum legal size limit provides a high yield while ensuring a high level of egg production (Cleaver 1949, Poole and Gotshall 1965, Methot 1986).

Tofino, B.C. was chosen as the main site for this two year study because of its accessibility and well-bounded fishery for C. magister. Tofino has been a traditional crab fishing region

for most of this century. Sampling in other coastal regions supplemented the information collected near Tofino. A two year old cohort of male and female C. magister was followed for 18 months as it matured, and in the case of males, entered the fishery. Spatial, temporal and size frequency distributions of sublegal-sized males and females were obtained from beam trawl samples. By applying size frequency analysis, which included information on moult increments-at-size, to beam trawl samples, the transition of smaller instars to larger instars was followed. Information on natural and fishing mortality, movement, growth, and the entry of males into the fishery was gathered from a mark-recovery program. Catch rates were determined by sampling trap catches on board commercial fishing vessels. The proportion of legal-sized males taken by the fishery was estimated by size frequency analysis on data from trap samples.

Trap generally provide size frequency data biased by the dynamics of entry and exit of crabs, changes in bait effectiveness over time, and agonistic interactions among crabs (Caddy 1979). To reduce such bias, experiments were performed to estimate parameters for models describing entry and exit rates as modified by changes in bait effectiveness and agonistic interactions. Experiments were also performed to measure retention probabilities for different sizes of crabs by different trap types. A general model of the dynamic interactions between

crabs and traps was constructed from the results of these experiments to help standardize data obtained from different trap types and after different soak times.

## 2 DESCRIPTION OF STUDY AREAS

Most field work was performed near Tofino, British Columbia. Sampling was limited to those waters enclosed by the dashed lines in Fig. 2.1, and included Lemmens Inlet, Browning Passage and the water surrounding Indian Island. These sites are within Statistical Area (SA) 24, as defined by the Canadian Department of Fisheries and Oceans, and support most of the fishery in SA 24. Statistical Area 24 accounted for 13 and 20% of the total weight of C. magister landed in British Columbia in 1985 and 1986, respectively. No crab fishing occurs in waters inland of this study area due to poor crab habitat. The fishery was exploited year-round, although some fishermen switched to crab fishing only after a summer of salmon fishing.

The waters of the study area are shallow ( $\approx 5\text{-}15$  m depth) and well mixed. The substrate varies from sand in the more exposed areas to mud at the head of Lemmens Inlet. Annual surface seawater temperature ranges from  $\approx 6\text{-}12^{\circ}\text{C}$ , but summer temperatures may reach  $18^{\circ}\text{C}$  in surface waters of upper Lemmens Inlet or near Indian Island. Although no larval settlement was detected during this study, the tradition of a productive crab fishery in this region may be due to the extensive mudflats (stippled area, Fig. 2.1) which provide high quality habitat for newly settled and first-year crabs (Armstrong and Gunderson 1985).

Information from three other regional fisheries is included in this study. The Dixon Entrance fishery (SA 1) is concentrated in shoal water north of the Queen Charlotte Islands (Fig. 2.1, Insert I, 'a') and accounted for 14 and 16% of reported landings in 1985 and 1986, respectively. The Holberg Inlet fishery (SA 27) is a small fishery near the northern end of Vancouver Island (Fig. 2.1, Insert II, 'a') and accounted for <1% of reported landings in 1985 and 1986. The Fraser delta fishery (SA 29) near Vancouver (Fig. 2.1, Insert II, 'b') accounted for 30 and 23% of reported landings in 1985 and 1986, respectively. Figures 2.2 and 3 describe historical trends in catch and effort, respectively, for all but the Holberg Inlet fishery. In the Holberg Inlet fishery annual landings seldom exceeded 5 t, and effort exceeded 200 days fishing only once (in 1971).

Time series analyses were performed on the landing and effort statistics for all but the Holberg Inlet fishery to test for trends over time. Time series intervention analysis (an ARMA(1,0) linear or trend intervention, see Noakes 1986) using the McLeod-Hipel algorithm (Hipel and McLeod 1987) found no significant ( $\alpha=.05$ ) trends in the landing statistics for the SA 24 (Tofino) fishery, or in the landing and effort statistics for the SA 29 (the Fraser delta) fishery. A significant trend would indicate a linear increase or decrease in the landing statistics over time. Similarly, there were no significant trends in the landing and effort statistics for the SA 1 (Dixon



Entrance) fishery. Both could be described by an ARMA(9,0) process with significant autocorrelation terms only at lags of 1 and 9 years, the term for the 9 year lag being negative.

The extent of the increase in effort in SA 24 ( $p < .05$  for an ARMA(0,1) linear intervention beginning in 1965) is misleading since in recent years the quality of effort has decreased due to a high turnover of fishermen (Jamieson 1985). Also, there are fewer experienced fishermen and fewer traps fished per fisherman (as determined from interviews of fishermen during this study). Most fishermen fished 50-150 traps. Two of the more established fishermen fished  $\approx 200$ -300 traps and one fished  $\approx 800$  traps.

Twenty-seven (27) and 59 vessels reported landings from SA 24 during 1985 and 1986, respectively. As evident in Fig. 2.4, the number of fishermen reporting landings from SA 24 has increased dramatically in recent years. Thirty (30) of the 59 vessels which landed crabs in 1986 are known to have fished in the study area, as determined by matching landing statistics with my knowledge of fishing activities. These 30 vessels accounted for approximately 80% of the 265 t landed from SA 24 in 1986.

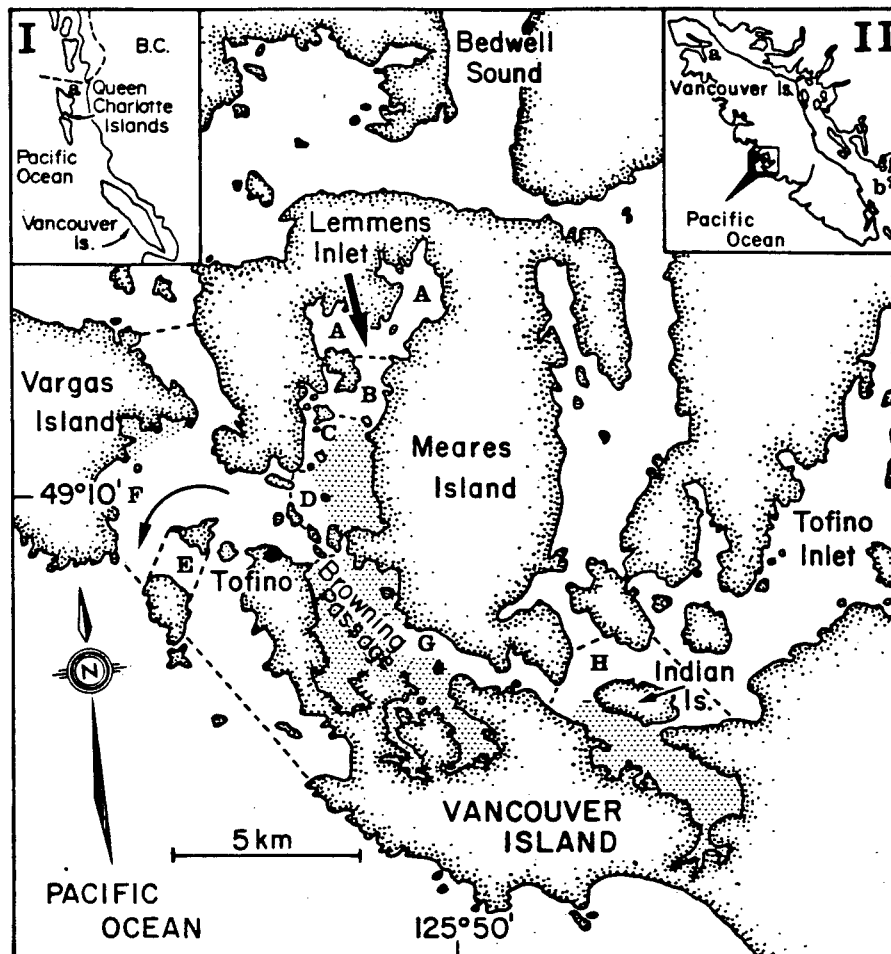
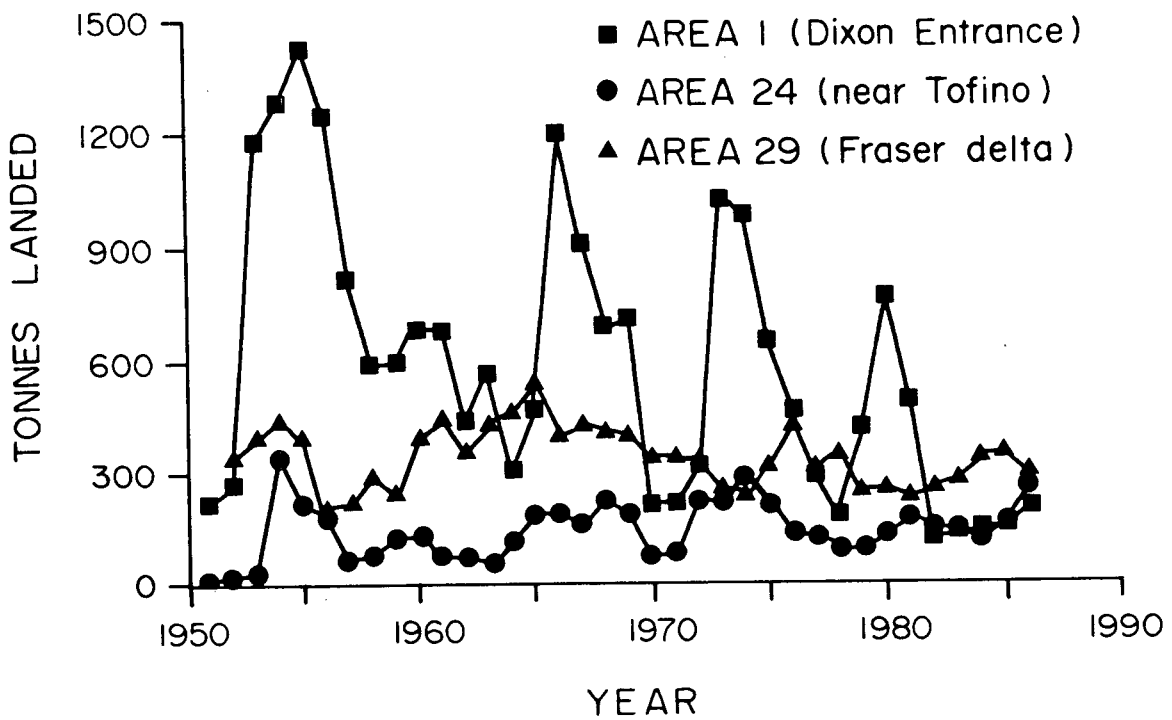


Figure 2.1. Map of the main study area near Tofino, British Columbia. The stippled areas are intertidal mudflats. The dashed lines delimit the main study area. Selected sites are referenced by capital letters. The arrow indicates the main channel out to sea. Insert I locates the Dixon Entrance fishery (a). Insert II locates the main study area, the Holberg Inlet fishery (a), and the Fraser delta fishery (b).




---

Figure 2.2. Time series of the annual tonnage of *C. magister* landed in the Statistical Area 1, 24 and 29 fisheries.

---

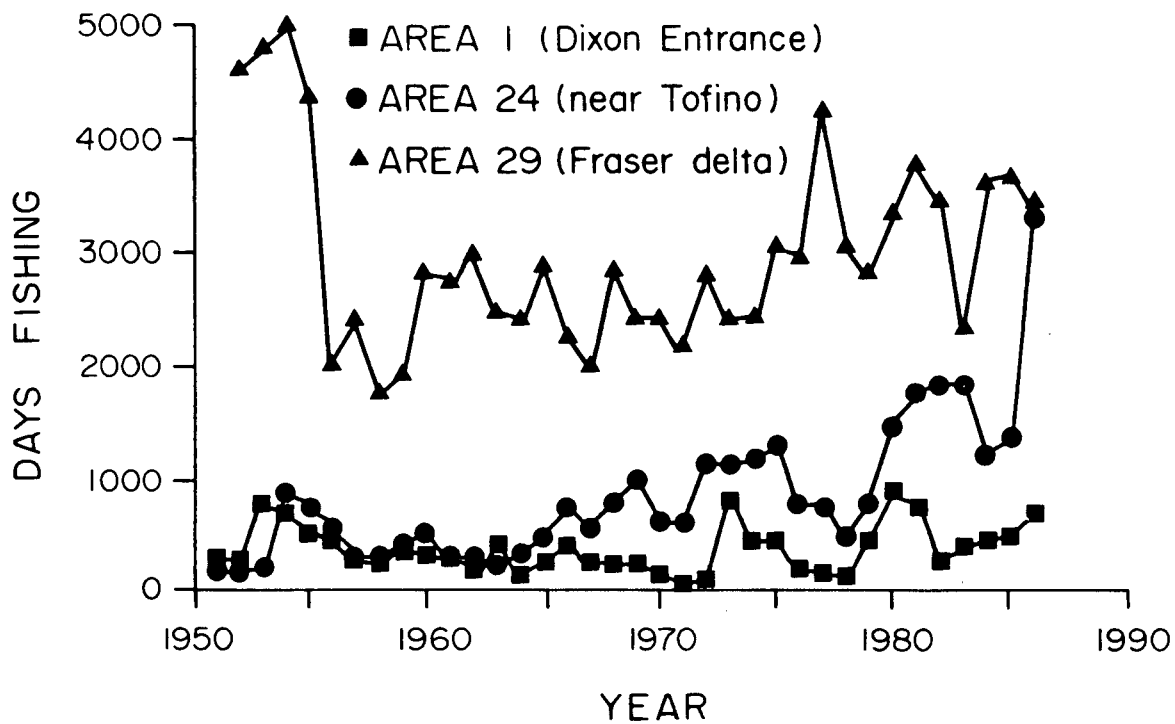
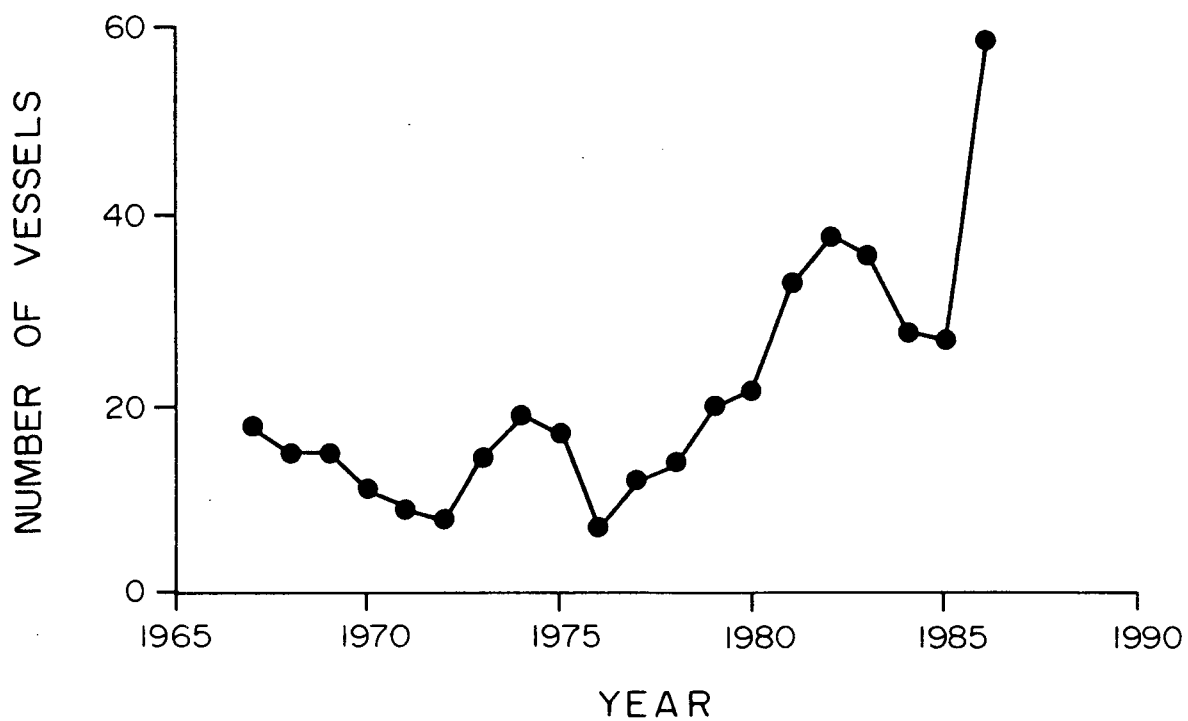


Figure 2.3. Time series of the annual number of days fishing for C. magister in the Statistical Area 1, 24 and 29 fisheries.



---

Figure 2.4. Time series of the annual number of vessels which reported landings of *C. magister* from the Statistical Area 24 fishery near Tofino, B.C.

---

### 3 FIELD METHODS

In order to evaluate the current minimum legal size limit for C. magister, a cohort of pre-recruit males and females was followed over time as the males entered the fishery and were subsequently exploited. Commercial fishing success, exploitation rates, spatial, temporal and size frequency distributions, size-at-maturity, and sizes of males and females in mating embraces were determined from sampling on board commercial and research vessels, and trawling. The trap samples were standardized by correcting for the effects of trap retention capabilities, changes in bait effectiveness, and agonistic interactions between crabs, based on experiments which analyzed these processes. Molt increments-at-size, length of intermolt periods, mortality, movement, and recruitment to the fishery were obtained from a mark-recovery program.

#### 3.1 MORPHOMETRICS

The standard measure of C. magister size is carapace width (CW) measured between the notches just anterior to the tenth anterolateral spines (notch-to-notch). Except where noted, carapace width refers to the notch-to-notch measurement truncated to the nearest millimeter. Trap standardization experiments required relationships to convert notch-to-notch carapace width to body length for both males and females. All crabs measured to determine these relationships were obtained near Tofino.

Because some earlier work measured carapace width between the tips of the tenth anterolateral spines (spine-to-spine), a relationship was established to convert spine-to-spine carapace width to the equivalent notch-to-notch measurement for the full range of male and female carapace widths observed. Spine-to-spine carapace width was determined from notch-to-notch carapace width by regression. Both measurements were obtained for at least one crab of each sex in each 1 mm interval from 100-190 and 100-170 mm CW, for males and females, respectively.

The size at which C. magister can be legally taken by fishermen is 165 mm CW (spine-to-spine, 154 mm notch-to-notch CW). The probability of a male of a particular notch-to-notch carapace width being legal size was determined from the joint distribution of notch-to-notch and spine-to-spine carapace widths for 100 crabs 152-156 mm CW (notch-to-notch). Twenty-five (25) crabs were measured within each 1 mm interval within this range.

Some analyses in this study required a measure of body length, so relationships converting notch-to-notch carapace width to body length for males and females were also established. In order to establish a relationship between notch-to-notch carapace width and body length for males and females, six pairs of measurements were taken for each 1 mm interval from 120-185 and 120-175 mm CW, for males and females, respectively. Body length was measured from the tip of the rostrum to the most posterior extension of the abdominal segments.

### 3.2 BEAM TRAWL SAMPLING

Spatial, temporal and size frequency distributions of mostly sublegal-sized male and female C. magister were obtained primarily by beam trawling. The trawl design was as described by Gunderson et al. (1985). The effective swept width is 2.3 m. The distance towed was determined by ranging landmarks at the beginning and end of a tow of 5-10 min, then estimating the distance towed from high resolution aerial photographs. Most tows were 200-500 m. Crab densities were estimated by dividing the number of crabs caught by the area swept by the beam trawl. Because beam trawls are not 100% efficient, densities should be interpreted only as indices of absolute abundance.

During summer 1985  $\approx 60$  tows assessed spatial distribution throughout the study area. In selected sites where crabs were abundant, tows were made at approximately monthly intervals from mid-1985 until September 1986. The date, tow depth, bottom type, and area swept were recorded. Details of specific trawls and their results are given in Section 4.11.

All crabs captured by beam trawling were identified to species. For C. magister, sex, shell hardness, and the presence of mating marks on male claws (Butler 1960), were noted; and carapace width was measured. A crab was considered hard-shelled if the exoskeleton of its legs could resist moderate pressure applied by the thumb and index finger.



### 3.3 TRAP SAMPLING

Size frequency distributions of male and female C. magister from commercial traps were determined by sampling the catch of commercial fishing vessels at approximately monthly intervals from April 1985 until September 1986. I accepted the invitation of four fishermen to sample on board their vessels. These data were complemented by fishing 'research' traps, which lacked escape ports, over the same time period. Research traps helped assess the abundance of smaller crabs which often were absent from commercial traps. The fishery was open to commercial fishing for the duration of this study. All crabs captured in traps were identified to species and assessed as in Section 3.2. Specific details of the trap sampling times and locations are given in Section 4.9.

Commercial C. magister catches were sampled in other regional fisheries between 1983 and 1986. The Holberg Inlet fishery was sampled in December 1984, and March and July 1986. The Dixon Entrance fishery was sampled in October of 1983 and 1984 (G.S. Jamieson, unpub. data). The Fraser delta fishery was sampled in October of 1984 and 1985 (P.A. Breen, unpub. data). The date, total number of traps hauled, location, soak time, trap type, and bait type, were recorded.

### 3.4 FEMALE SIZE-AT-MATURITY

From June 1985 until September 1986 females >80 mm CW collected in traps or trawls near Tofino were dissected to

determine if a pair of sperm packs, placed by a male during mating, was present in their spermathecae (Butler 1960). At least 10 females in each 5 mm interval from 80-160 mm CW were dissected. In March and July 1986  $\approx$ 50 large females collected in Holberg Inlet (SA 27) were also dissected.

### 3.5 MATING PAIRS

When mating pairs of C. magister were collected in traps or trawls, carapace widths of both individuals were measured. Mating pairs are easily recognized as a male clasping a smaller female with her abdomen against his (Butler 1960, Snow and Neilsen 1966). When convenient, the pair was retained and monitored in an enclosure until mating was complete to obtain pre- and post-moult carapace widths from the female.

### 3.6 TRAP DISTRIBUTION

The number of crab traps fished in the study area was determined by interviewing fishermen at approximately monthly intervals from June 1985 until September 1986. Because fishermen generally fish specific sites (e.g. Lemmens Inlet, Browning Passage, near Indian Island) trap distribution was also assessed.

To verify information from fishermen, the number of traps reported fished in Lemmens Inlet was compared with the number of trap buoys counted there each month for the duration of the study. With few exceptions each trap buoy indicated one trap. Traps were counted during calm weather from a moving boat.

### 3.7 TRAP PERFORMANCE EXPERIMENTS

Several processes contribute to the number, sex ratio and size frequency distribution of crabs within traps. Experiments were performed to measure the following processes for the purpose of standardizing commercial samples with different soak times.

1. The escape of crabs from traps as a function of carapace width.
2. The reduction in the entry rate of crabs into traps due to agonistic interactions among crabs.
3. The reduction in the entry rate of crabs into traps due to changes in bait effectiveness.

Performing these experiments within the two bays in upper Lemmens Inlet and near Indian Island (A,H; Fig. 2.1, page 9) assured excellent working conditions and easy execution of experimental activities, e.g. setting and maintaining grid patterns, trap hauling, crab measurement and data recording. These two locations were fished commercially, the Indian Island site being more productive.

The water depth at these locations was  $\approx 7-12$  m. Traps used in these experiments were set in grid patterns (Fig. 3.7.1) with a distance between adjacent traps of  $\approx 75$  m. Approximately 0.5 kg per trap of geoduck clam (Panope abrupta (Randall)) was used for bait. Geoduck was the choice of most commercial fishermen.

# GRID LAYOUT FOR TRAPPING EXPERIMENTS

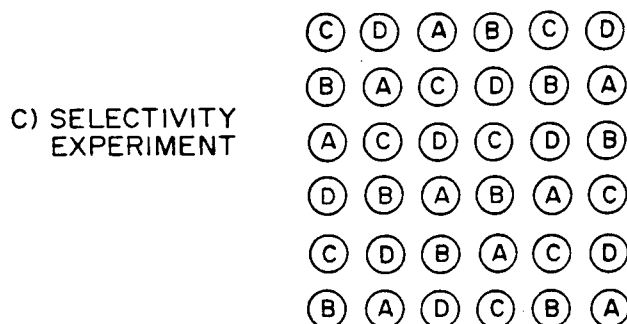
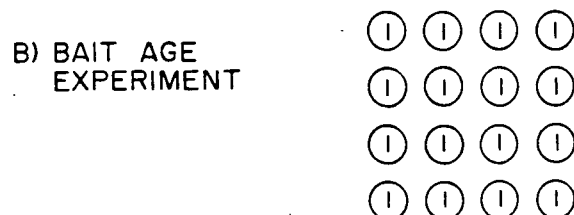
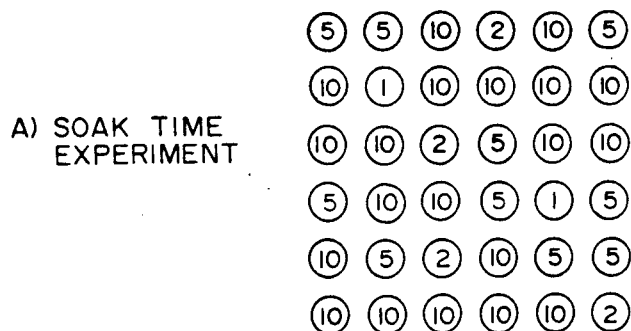


Figure 3.7.1. Layout of trap grids designed to emphasize the effects of different soak times (A), changes in bait effectiveness (B), and trap selectivity (C), on the density and size frequency distribution of C. magister. For (A) and (B) soak time (in days) is encircled, for (C) trap type is encircled.

### 3.7.1 TRAP TYPES

The basic commercial trap is circular with stainless steel or rubber-wrapped iron frames ranging in diameter from 90-105 cm. Trap height is 25 cm. Two iron weight bars placed on the bottom of a trap give it a weight of 15-25 kg. Two diametrically opposed 21-25 by 10 cm entrance tunnels recessed 25 cm from the trap perimeter require a crab to ascend a 20° slope to enter the trap. Two one-way triggers opening toward the center of the trap prohibit an easy exit. Traps are enclosed by a 1 mm stainless steel wire mesh forming a 7 by 4 cm diamond configuration. Bait is placed in the center of the trap in a perforated 500 mL plastic jar. The bait jar is replaced and crabs removed by opening a fold-over trap lid normally held shut by a hook on a stretched rubber strap. Photographs of traps of this general design can be seen in High (1976a) and Miller (1978, 1979).

Four trap types were distinguished by the number and inside diameter of their escape ports. Escape ports are located high in the side of a trap perpendicular to the entrance tunnels. Paired escape ports are diametrically opposed.

Trap A	No escape ports (research traps)
Trap B	1 102.5±0.5 mm escape port
Trap C	1 109.2±1.5 mm escape port
Trap D	2 109.2±1.5 mm escape ports

Trap A is not legal for commercial fishing but was used in all grid experiments to achieve higher retention of smaller crabs. Traps B and D are legal for commercial fishing and were

used locally by the fishermen whose catch I sampled. Although not used locally, Trap C was included in a selectivity experiment (Section 3.7.3) to provide an intermediate escapement between Traps B and D.

### 3.7.2 CATCH RATES OF TRAPS IN GRIDS

The following fishing experiments which use a grid sampling format assume that all traps in a grid are equivalent sampling units. By comparing the catch rates of the perimeter and interior traps in a grid, this assumption was tested. In July 1985 two 5 by 5 grids were arranged in each of the two bays in upper Lemmens Inlet (A; Fig. 2.1, page 9). After a 24 h soak all traps in both grids were hauled. For each trap, all crabs were assessed as in Section 3.2, and the trap location in the grid was recorded.

### 3.7.3 ESCAPE OF CRABS FROM TRAPS

The percent of C. magister escaping Trap A in 24 h was estimated by tagging several apparently healthy crabs, placing them in a trap, then counting the number remaining after a 24 h soak. After each trap haul untagged crabs were tagged and, along with previously tagged crabs, monitored for a successive 24 h period. The tagging procedure is described in Section 3.8. Crabs with tags that were retained by a trap for 24 h were presumed to represent independent observations for the next 24 h

period. For example, observing a tagged crab in a trap for five consecutive days is considered equivalent to having observed five different crabs after 24 h.

Traps were loaded to typical densities ( $\approx 5$ -10 per trap) and placed in a 5 by 5 grid in upper Lemmens Inlet, or in pairs near Indian Island (A,H; Fig. 2.1, page 9), at  $\approx 7$ -10 m depth. This experiment was performed intermittently from June-August of 1985 and 1986 with traps being hauled for up to 10 consecutive days. Performing this experiment in different locations, without changing the bait and 'reusing' tagged crabs, helped reduce biases that may have resulted if only fresh bait, newly captured crabs, or a single site were consistently used. Thus, these escapement rates should be generally applicable to the commercial fishery throughout the study area.

The selectivities of Traps B-D relative to Trap A were determined by simultaneously fishing nine traps of Traps A-D in a regular pattern in a 6 by 6 grid (Fig. 3.7.1c). Each day, for seven days, all 36 traps were hauled after a 24 h soak, the bait changed and traps replaced. All crabs in each trap type were assessed as in Section 3.2.

#### 3.7.4 SOAK TIME EXPERIMENT

A 6 by 6 grid (Fig. 3.7.1a) was used to determine the densities and size frequency distributions of C. magister within Trap A traps hauled after soak times of 1, 2, 5 and 10 days. This grid was arranged in upper Lemmens Inlet in August 1985 and

near Indian Island in June 1986. The encircled numbers indicate randomly distributed soak times for traps composing the grid. Twenty (20) hauls were made for each soak time trial by hauling the appropriate traps on 10 consecutive days according to the following schedule.

1. Two 1 day soak traps hauled every day.
2. Four 2 day soak traps hauled every second day.
3. Ten 5 day soak traps hauled every five days.
4. Twenty 10 day soak traps hauled after 10 days.

A separate 5 by 4 grid was arranged 20 days prior to the previously described grid to provide 20 replicates for a 20 day soak. Because the 20 day trial was not fished simultaneously with the shorter soak time trials, it was repeated after the shorter soak time trials to assess any trend in the catch rate over time. No differences were evident so the earlier trial was used in both the 1985 and 1986 experiments.

After each trap haul crabs were released and the bait was changed. All crabs were assessed as in Section 3.2. Traps were replaced where they were hauled.

#### 3.7.5 BAIT-EFFECTIVENESS EXPERIMENT

Changes in densities and size frequency distributions of crabs within Trap A resulting from changes in bait effectiveness were assessed over the same 10 day time period as the 1, 2, 5 and 10 day soak time trials (Section 3.7.4). The 4 by 4 grid used for this experiment (Fig. 3.7.1b) was arranged near the 6 by 6 soak time grid in upper Lemmens Inlet in August 1985 and near



Indian Island in June 1986. In upper Lemmens Inlet the soak time and bait age experiments were separated by 2 km, with one grid in each of the two bays (A; Fig. 2.1, page 9). Near Indian Island the two grids were within 200 m of each other (H; Fig. 2.1). Both grids at each site were presumed to sample crab populations with similar size frequency distributions.

At the beginning of the experiment all 16 traps were set with fresh bait. After 24 h, for eight consecutive days, all 16 traps were hauled, the crabs released, and the traps replaced without changing the bait. On the ninth day the bait jar was removed and the traps replaced without bait. All crabs were assessed as in Section 3.2.

### 3.8 MARK-RECOVERY PROGRAM

Male and female C. magister were tagged and released between April 1985 and May 1986. Most males were sublegal size, all females were sublegal size. Release and recovery locations were determined with a grid identification system (0.9 by 1.2 km) and landmarks. Crabs for tagging were obtained from 'research' traps, fishermen, or trawling. Before being released, the date, location and tag number were recorded. Crabs were assessed as in Section 3.2.

Blue, individually numbered, 4.1 cm anchor tags (Floy Tag and Manufacturing Co., P.O. Box 5357, Seattle, Washington, U.S.A.) were inserted gently through the right posterior epimeral suture line with a tagging gun, taking care not to puncture

internal organs. The colour blue was chosen for the tags because it contrasted well with the natural colouration of C. magister, thereby increasing visibility. Placing the tag through the epimeral suture line is assumed to assure a high retention rate when the old shell is discarded during a moult. To test this assumption, tag retention was assessed by double tagging 850 sublegal-sized male C. magister. Two tags were inserted as described above except that the second tag was inserted through the left posterior epimeral suture line.

Most recoveries were obtained from fishermen and research traps. Four fishermen recorded the date, location and tag number of all tagged crabs they recovered on special forms. Three fishermen also measured carapace width using calipers. Females and sublegal-sized males were released, but legal-sized males were generally retained. Whether a crab was retained or released was recorded by the fishermen. Most other fishermen generally ignored recoveries of sublegal-sized crabs, but retained tags from legal-sized males. The extent of information provided with a tag return varied among fishermen. Tags were either given to me or an associate, or I had permission to board a fisherman's vessel at the dock and retrieve tags set aside. Some fishermen kept tagged legal-sized males in live wells until I could measure them.

The information obtained from a tag recovery was sometimes supplemented by my knowledge of where particular fishermen fished, and the frequency with which I checked with them

regarding recoveries. From April until August in 1985 and 1986 I saw most fishermen at least biweekly, at other times, monthly. I increased the number of tag recoveries by attending dock side buying and sorting sessions. One major buyer, Tri-Star Seafood Supply Limited of Vancouver, B.C. recovered tags from crabs they purchased and mailed them to me.

## 4 RESULTS

### 4.1 SPECIES COLLECTED

Three Cancer spp. were collected in traps and beam trawls. C. productus Randall, the red rock crab, and C. gracilis Dana, the graceful crab, accounted for <5% of the total catch by these methods, although in certain areas they were more abundant. Only C. magister was considered in the following analyses.

### 4.2 MORPHOMETRICS

Notch-to-notch carapace width (CW, mm) is determined from spine-to-spine carapace width (S, mm) for male and female C. magister, respectively, by the following linear relationships (SAS Institute Inc. 1985) valid for all observed carapace widths.

Males:

$$CW = 0.937 \cdot S; p < .0001, r^2 > 99.9\%, n = 509 \quad (4.2.1)$$

Females:

$$CW = 0.950 \cdot S; p < .0001, r^2 > 99.9\%, n = 478 \quad (4.2.2)$$

The probability of a male, whose carapace width was measured notch-to-notch, exceeding the minimum legal size limit of 165 mm CW (spine-to-spine) was determined from the proportion of males >165 mm CW (spine-to-spine) for 25 crabs within each 1 mm CW interval from 152-156 mm (notch-to-notch).

The probability of a male being legal size when its notch-to-notch carapace width lies within a 1 mm interval between 153-155 mm CW is listed below.

Male notch-to-notch <u>carapace width (mm)</u>	Probability of being <u>legal size</u>
<153	0.00
153-154	0.40
154-155	0.72
>155	1.00

The following linear relationships between notch-to-notch carapace width (CW, mm) and body length (L, mm) are valid for 120-185 and 120-175 mm CW, for male and female C. magister, respectively. Some extrapolation of these relationships beyond these ranges will not introduce significant error.

Males:

$$L = 4.95 + 0.677 \cdot CW; p < .0001, r^2 = 98.4\%, n = 390 \quad (4.2.4)$$

Females:

$$L = 1.94 + 0.718 \cdot CW; p < .0001, r^2 = 95.5\%, n = 330 \quad (4.2.5)$$

#### 4.3 FEMALE SIZE-AT-MATURITY

In this study all females >115 mm CW up to the largest size dissected of 180 mm CW had been mated regardless of the location or the time of year when they were collected (Fig. 4.3.1). In the Holberg Inlet fishery, where large females were most abundant, all of  $\approx 50$  large (150-180 mm CW) females dissected contained a pair of sperm packs.

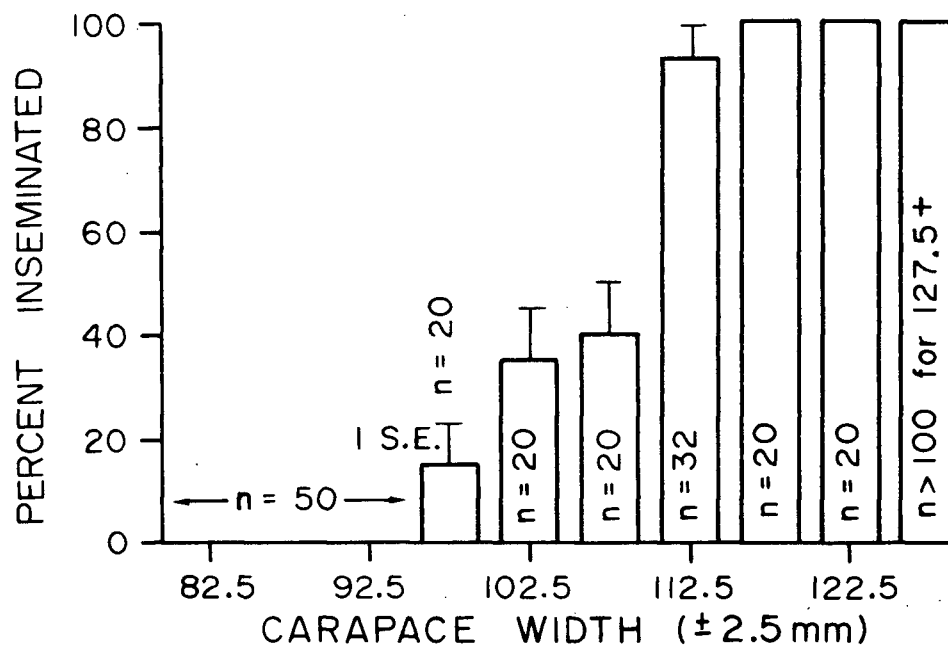


Figure 4.3.1. The percent of female *C. magister* inseminated as a function of carapace width.

#### 4.4 MATING PAIRS

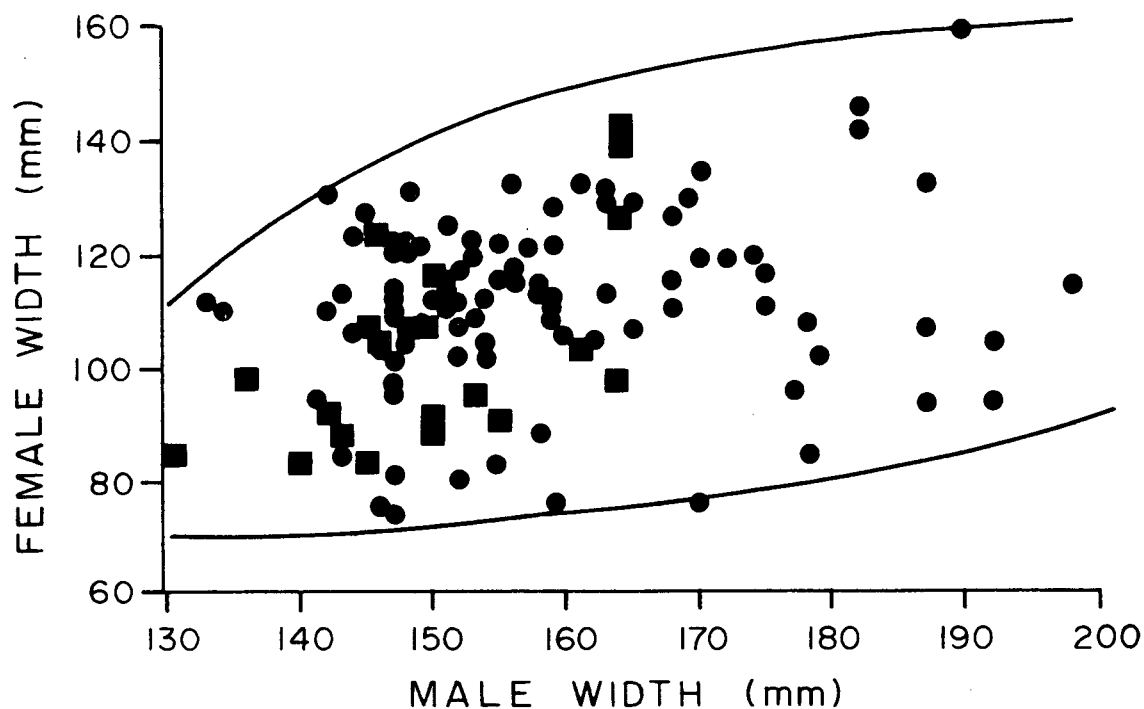
Twenty-one (21) mating pairs of C. magister were measured between April 1985 and September 1986. These were supplemented by 97 mating pairs measured by T.H. Butler (unpub. data) in Dixon Entrance during the 1950's. Figure 4.4.1 presents a scatter plot of male versus female carapace widths for mating pairs. As suggested by these data, the lines represent limits of male (MCW) and female (FCW) carapace width combinations apparently necessary for a mating embrace to occur. Males are considered functionally mature near 130 mm CW and females are considered mature near 70 mm CW (Butler 1960). Size frequency distributions from Butler (1961) and this study (Fig. 4.6.1, page 37) suggest that Fig. 4.4.1 represents mating preferences, not restricted availability of females.

Upper line:

$$FCW = 165.0 \cdot \{1.0 - \exp[-0.04 \cdot (MCW - 105.0)]\} \quad (4.4.1)$$

Lower line:

$$FCW = 70.0 + \exp[0.045 \cdot (MCW - 130.0)] \quad (4.4.2)$$




---

Figure 4.4.1. Carapace widths of *C. magister* mating pairs. The lines (Eqns. 4.4.1 and 2) define the apparent limits in carapace widths required for a mating embrace. Circles represent data from Butler (unpub. data), squares represent data from this study.

---



#### 4.5 MOULT INCREMENTS

Relationships between carapace width and moult increments-at-size for male and female C. magister were obtained from pre- and post-moult carapace width measurements. The number of records is small (76 for males, 7 for females), and within a limited pre-moult carapace width range, so they were supplemented with equivalent data from four other published sources. Because Butler (1961) summarized moult increments-at-size for Dixon Entrance by 5 mm CW intervals, they are reanalysed using regression analysis. From California, Collier (1983) and Warner (1987) provide moult increments-at-size for males, and Diamond (1983) provides moult increments-at-size for females. The regression analyses (SAS Institute Inc. 1985) for these data are presented in Tables 4.5.1 and 2, for males and females, respectively.

Analysis of covariance indicated significant ( $p < .05$ ) differences between the regression models for the different male and female data sets. However, for two reasons this is not considered sufficient to reject the two models based on all male (Eqn. 4.5.1) and all female (Eqn. 4.5.2) data combined (Figs. 4.5.1 and 2). Authors used different measuring techniques, and the maximum differences between the model predictions for the individual data sets, and those of the combined data sets, are  $< 2$  mm, and only at the low extreme of the range sampled.

Table 4.5.1. Linear regression models for male C. magister moult increments-at-size for four data sets collected from British Columbia (B.C.) and California (Cal.).

<u>Model equation</u> <sup>a</sup>	<u>n</u>	<u>p</u>	<u>r<sup>2</sup>(%)</u>	<u>Region</u>	<u>Source</u>
I = 19.72+0.059·CW	277	<.0001	11.8	B.C.	Butler (1961)
I = 15.78+0.078·CW	72	.0090	9.4	Cal.	Collier (1983)
I = 16.50+0.078·CW	19	.0794	1.7	Cal.	Warner (1987)
I = 21.19+0.046·CW	76	.1751	2.5	B.C.	This study
I = 18.07+0.069·CW (Eqn. 4.5.1)	444	<.0001	11.3		All data sets <sup>b</sup>

<sup>a</sup> I is the moult increment-at-size (mm).

CW is the pre-moult carapace width (mm).

<sup>b</sup> The standard deviation of the estimate for the intercept is 1.26, for the slope, 0.009.

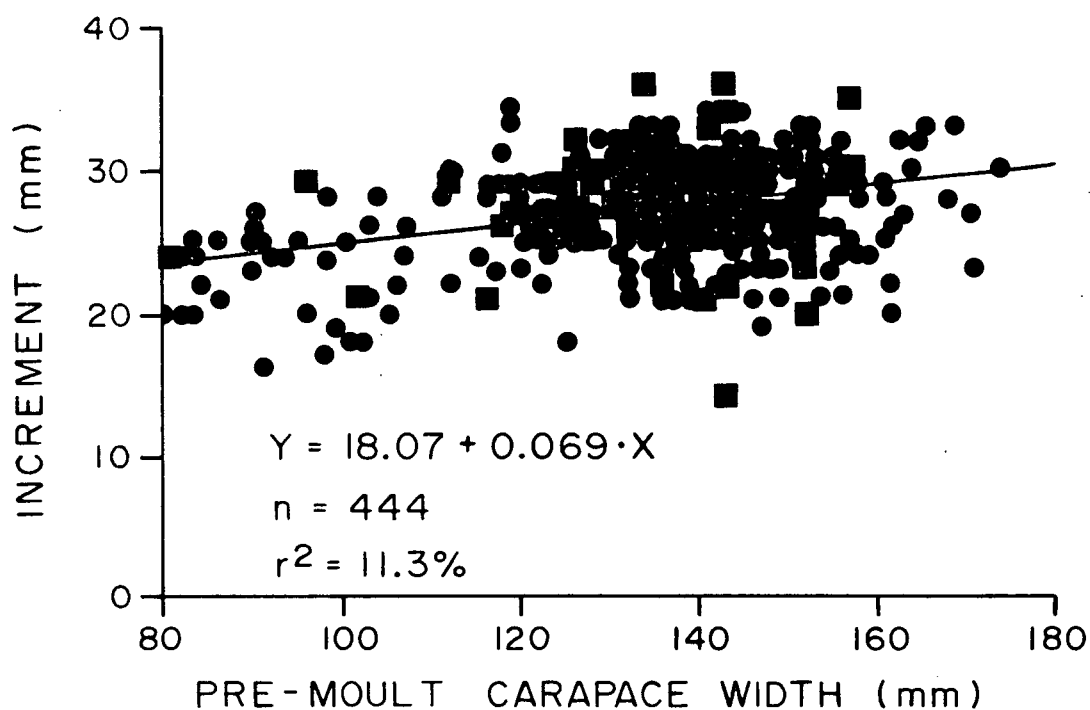
Table 4.5.2. Linear regression models for female C. magister moult increments-at-size for three data sets collected from British Columbia (B.C.) and California (Cal.).

<u>Model equation</u> <sup>a</sup>	<u>n</u>	<u>p</u>	<u>r<sup>2</sup>(%)</u>	<u>Region</u>	<u>Source</u>
I = 28.63-0.100·CW	44	.0006	24.6	B.C.	Butler (1961)
I = 32.11-0.135·CW	277	<.0001	43.5	Cal.	Diamond (1983)
I = 27.77-0.105·CW	7	.0567	54.9	B.C.	This study
I = 32.35-0.136·CW (Eqn. 4.5.2)	328	<.0001	46.0		All data sets <sup>b</sup>

<sup>a</sup> I is the moult increment-at-size (mm).

CW is the pre-moult carapace width (mm).

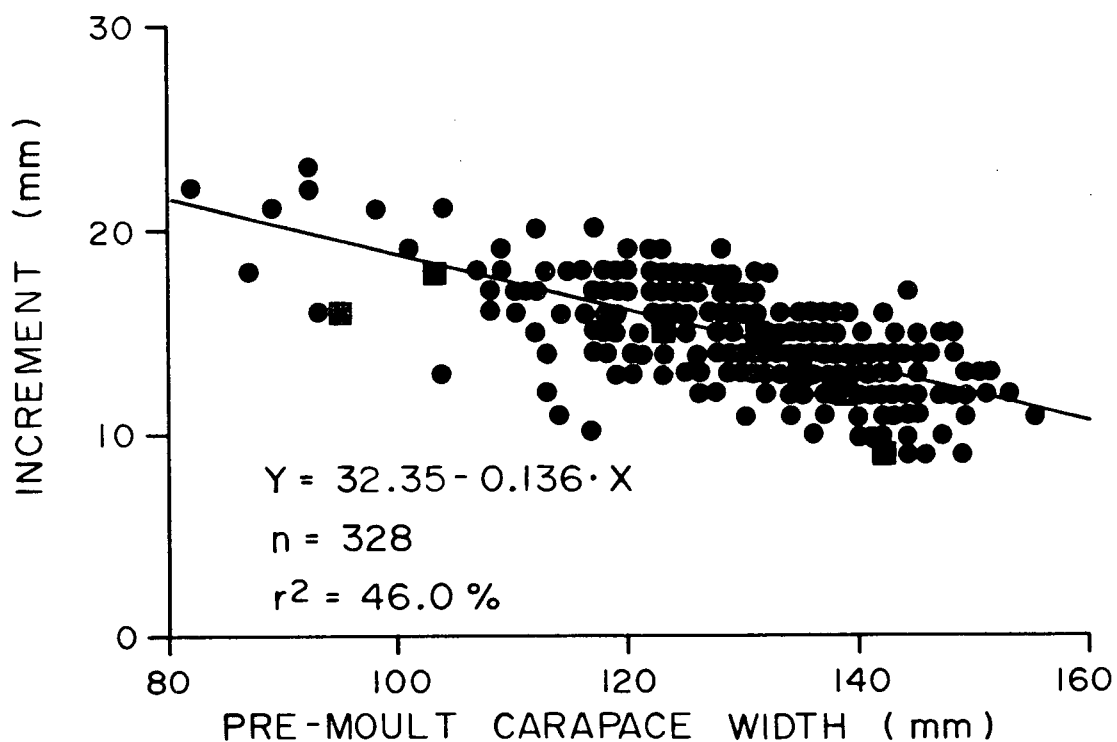
<sup>b</sup> The standard deviation of the estimate for the intercept is 1.076, for the slope, 0.008.



---

Figure 4.5.1. Male *C. magister* moulting increments as a function of pre-moulting carapace width. The plot uses data from British Columbia and California. Data from this study are represented by squares.

---



---

Figure 4.5.2. Female *C. magister* moult increments as a function of pre-moult carapace width. The plot uses data from British Columbia and California. Data from this study are represented by squares.

---

#### 4.6 GROWTH

Instar mean sizes and standard deviations for C. magister were determined from size frequency analyses of the carapace widths of crabs caught in beam trawl samples. To increase the sample size, and thus the power of the size frequency analyses, all data from crabs caught in beam trawls from June 1985 until September 1986 were combined to create single distributions (1 mm CW interval) for each sex. The distributions are summarized by 5 mm CW intervals in Fig. 4.6.1.

Cancer magister grows by moulting from one instar to a larger instar. The size distribution of crabs within any instar shows natural variability and it is generally presumed that instars are normally distributed and can be described by a mean and standard deviation (e.g.  $155.0 \pm 11.2$  mm CW). Since C. magister grows discontinuously by increments, with one instar decomposing and subsequently forming a new instar at a larger size, combining samples taken at different times should not confound these normal distributions. Only crabs >80 mm CW were used because Butler (1961) and Collier (1983) show that the relationship between the size of a moult increment and carapace width is nonlinear when crabs <80 mm CW are included.

Data from crabs collected in traps were not used to analyze growth because the size frequency distributions obtained from trap samples were strongly biased by differences in the soak time that trap samples experienced (e.g. see Section 4.7.3).

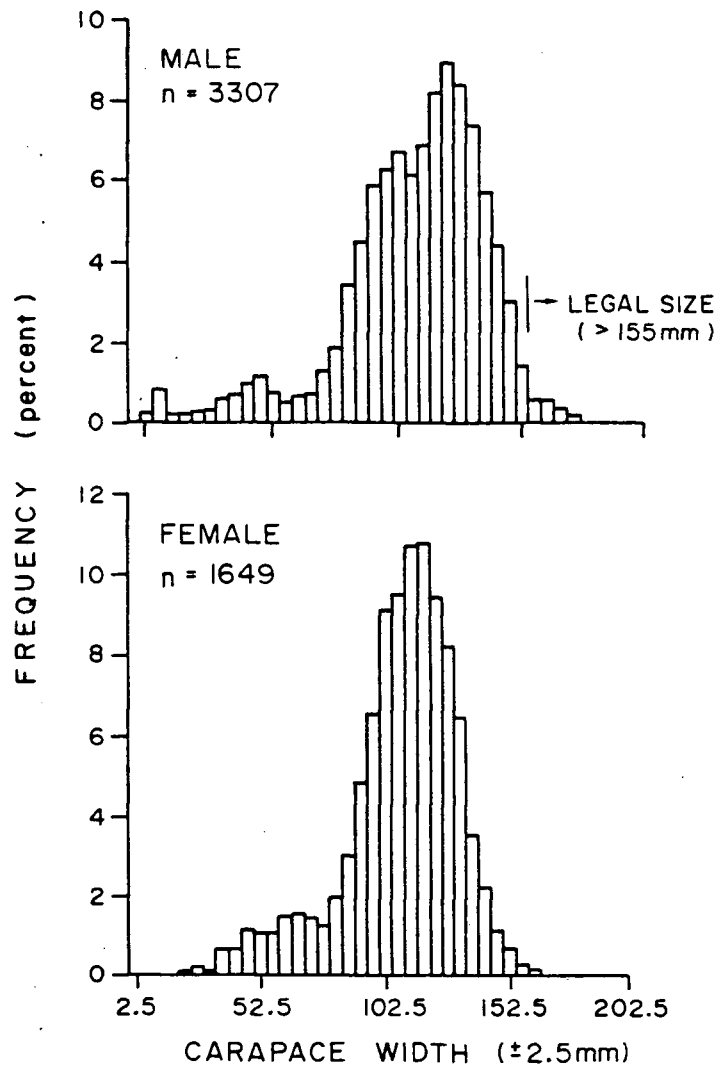


Figure 4.6.1. Size frequency distributions for all male and female *C. magister* collected in beam trawl samples from June 1985 until September 1986.

The size frequency analyses were based on the methodology of Schnute and Fournier (1980), and include the linear equations for male and female growth increments-at-size (Eqns. 4.5.1 and 2 in Tables 4.5.1 and 2, page 33). The standard deviation (D) of an instar mode was modeled as a function of the consecutive instar number (N) for modes recognized by the model, where 'd' is the standard deviation for N=1.

Males:

$$D = d \cdot 1.069(N-1) \quad (4.6.1)$$

Females:

$$D = d \cdot 0.864(N-1) \quad (4.6.2)$$

The constants of 1.069, for males, and 0.864, for females, are equal to the slope+1 in Eqns. 4.5.1 and 2, and presume that the standard deviations for particular instars vary with the moult increment-at-size. These equations provided the most suitable results of those assessed, and they facilitated easy simulation of instar growth in the yield- and eggs-per-recruit model (Section 5).

For each analysis there is one unknown parameter in the growth equation (i.e. the mean carapace width for the first instar recognized by the size frequency model), and one unknown parameter in the equations relating standard deviation to instar number (i.e. the standard deviation for N=1). Subsequent instars are defined in relation to the first instar by the growth and standard deviation equations. Additional parameters estimate the

proportions-at-age for each instar recognized by the model. The size frequency analysis for males included an additional parameter measuring size-specific exploitation of legal-sized males. The probabilities of males between 152-156 mm being legal size are listed in Section 4.2.

Parameter estimates were obtained using the SIMPLEX nonlinear estimation package (Mittertreiner and Schnute 1985). A maximum likelihood objective function, the separation statistic 'A' of Schnute and Fournier (1980), was used to evaluate the parameter estimates. Male and female instars determined by the size frequency analyses are defined in Tables 4.6.1 and 2. Subsequently, the relative proportions of male and female instars within a time series of beam trawl samples (Tables 4.6.3 and 4) were determined from size frequency analyses using Eqns. 4.5.1 and 2 and Eqns. 4.6.1 and 2 to define the means and standard deviations of the instars, respectively. The parameter estimates for 'd' in Eqns. 4.6.1 and 2 were taken from Tables 4.6.1 and 2.

The 102.9 mm male instar dominated the beam trawl samples from July-December 1985, then moulted into the 128.0 mm instar by late spring 1986. The moulting of this instar into the 155.0 mm instar throughout the remainder of 1986 was assessed by the mark-recovery program (Section 4.13). The 100.7 mm female instar present from June-September 1985 moulted into the 119.4 mm instar by January 1986. This instar moulted into the 135.5 mm instar in summer 1986, suggesting females this size moult only once annually. Since females mate only following their moult (Butler



1960), this suggests peak mating activity occurs during summer. Few males or females 80-120 mm CW were present during summer 1986. Crabs this size are two years old (post-settlement) (Butler 1961, Stevens and Armstrong 1984) suggesting there was either little larval settlement or survival in 1984.

---

Table 4.6.1. Mean and standard deviations (SD, sd) for carapace widths defining instars of male C. magister >80 mm CW.

---

<u>Instar</u>	<u>Mean</u>		<u>SD</u>		<u>Proportion<sup>a</sup></u>
	<u>Estimate</u>	<u>sd</u>	<u>Estimate</u>	<u>sd</u>	
1	79.3	0.3	9.2	0.2	0.071
2	102.9	-	9.8	-	0.295
3	128.0	-	10.5	-	0.445
4	155.0	-	11.2	-	0.188
5 <sup>b</sup>	183.8	-	12.0	-	-

---

<sup>a</sup> The proportion of males in the combined beam trawl samples contributed by each instar.

<sup>b</sup> Determined by extrapolation.

---



---

Table 4.6.2. Mean and standard deviations (SD, sd) for carapace widths defining instars of female C. magister >80 mm CW.

---

<u>Instar</u>	<u>Mean</u>		<u>SD</u>		<u>Proportion<sup>a</sup></u>
	<u>Estimate</u>	<u>sd</u>	<u>Estimate</u>	<u>sd</u>	
1	79.1	4.6	14.8	2.6	0.001
2	100.7	-	12.8	-	0.386
3	119.4	-	11.0	-	0.529
4	135.5	-	9.5	-	0.067
5	149.4	-	8.2	-	0.016
6 <sup>b</sup>	161.4	-	7.1	-	-

---

<sup>a</sup> The proportion of females in the combined beam trawl samples contributed by each instar.

<sup>b</sup> Determined by extrapolation.

---

Table 4.6.3. The relative proportions of male C. magister >80 mm CW within consecutive instars for a time series of beam trawl samples. The value for each date includes all males captured within two weeks of that date. The dominant instar is highlighted by an asterisk.

<u>Date</u>	<u>Sample size</u>	Instar mean carapace width (mm)			
		<u>79.3</u>	<u>102.9</u>	<u>128.0</u>	<u>155.0</u>
21 Jun 1985	97	0.42*	0.23	0.08	0.26
11 Jul 1985	255	0.15	0.73*	0.02	0.10
14 Aug 1985	147	0.14	0.69*	0.04	0.13
11 Sep 1985	115	0.00	0.84*	0.00	0.16
16 Oct 1985	290	0.00	0.64*	0.35	0.01
4 Dec 1985	143	0.04	0.48*	0.37	0.10
8 Jan 1986	202	0.02	0.41	0.56*	0.00
4 Feb 1986	245	0.01	0.24	0.42*	0.33
5 Mar 1986	581	0.00	0.10	0.73*	0.16
8 Apr 1986	280	0.02	0.08	0.62*	0.27
7 May 1986	318	0.01	0.11	0.61*	0.27
4 Jun 1986	199	0.03	0.21	0.71*	0.06
11 Jul 1986	41	0.00	0.21	0.50*	0.28
6 Aug 1986	27	0.00	0.13	0.19	0.68*
9 Sep 1986	32	0.02	0.05	0.18	0.75*

Table 4.6.4. The relative proportions of female C. magister >80 mm CW within consecutive instars for a time series of beam trawl samples. The value for each date includes all females captured within two weeks of that date. The dominant instar is highlighted by an asterisk.

<u>Date</u>	<u>Sample size</u>	Instar mean carapace width (mm)				
		<u>79.1</u>	<u>100.7</u>	<u>119.4</u>	<u>135.5</u>	<u>149.4</u>
21 Jun 1985	76	0.24	0.53*	0.14	0.09	0.00
11 Jul 1985	226	0.00	0.83*	0.14	0.00	0.02
14 Aug 1985	167	0.00	0.97*	0.00	0.02	0.01
11 Sep 1985	130	0.00	0.66*	0.32	0.01	0.00
16 Oct 1985	173	0.01	0.28	0.71*	0.00	0.00
4 Dec 1985	119	0.14	0.13	0.73*	0.00	0.00
8 Jan 1986	95	0.00	0.01	0.99*	0.00	0.00
4 Feb 1986	62	0.05	0.02	0.90*	0.03	0.00
5 Mar 1986	56	0.01	0.00	0.70*	0.30	0.00
8 Apr 1986	35	0.05	0.00	0.95*	0.00	0.00
7 May 1986	77	0.00	0.00	0.69*	0.31	0.00
4 Jun 1986	38	0.08	0.00	0.92*	0.00	0.01
11 Jul 1986	20	0.05	0.00	0.55*	0.40	0.00
6 Aug 1986	11	0.00	0.12	0.77*	0.11	0.00
9 Sep 1986	177	0.00	0.01	0.05	0.53*	0.40

## 4.7 TRAP PERFORMANCE EXPERIMENTS

### 4.7.1 CATCH RATES OF TRAPS IN GRIDS

Analysis of variance compared (1) the number of C. magister caught in 16 perimeter and nine interior traps within two 5 by 5 grids in the two bays in upper Lemmens Inlet, and (2) the mean catch rates for each grid. No significant differences within or between grids were detected (Table 4.7.1.1). Kolmogorov-Smirnov tests (Sokal and Rohlf 1981) could not detect that (1) the distribution of the number of crabs per trap deviated significantly ( $p > .1$ ) from a normal distribution, and (2) the distribution of the number of crabs per trap was significantly ( $p > .1$ ) different for interior versus perimeter traps in either grid. Therefore, interior and perimeter traps, and the traps of each grid, were considered equivalent sampling units.

---

Table 4.7.1.1. Comparison of the mean number of C. magister caught per trap for 16 perimeter versus nine interior traps in two 5 by 5 grids, and between all traps in each grid.

---

	<u>Interior</u>			<u>Perimeter</u>			$p^a$
	<u>Mean</u>	<u>SD</u>	<u>Range</u>	<u>Mean</u>	<u>SD</u>	<u>Range</u>	
Grid 1	5.7	1.6	5-10	6.5	2.7	3-14	>.1
Grid 2	6.9	2.4	3-10	6.5	3.3	0-12	>.1

---

	<u>Grid 1</u>			<u>Grid 2</u>			
Grid 1 vs. Grid 2	6.2	2.4	3-10	6.6	2.9	0-14	>.1

---

<sup>a</sup> The probability that the above results are obtained given there is no difference in catch rate for perimeter and interior traps, and between traps in Grid 1 and Grid 2.

---

#### 4.7.2 ESCAPE OF CRABS FROM TRAPS

The percent of tagged male C. magister retained within Trap A ('research' traps) for 24 h is shown for 5 mm intervals ranging from 135-170 mm CW in Fig. 4.7.2.1. Crabs 120-135 and 170-190 mm CW were combined into larger intervals of 15 and 20 mm, respectively, because there were no apparent differences in retention over these size ranges. Traps are not effective in retaining crabs <135 mm CW because they easily enter and exit traps through the mesh and entrances. Between 135-170 mm CW increasing percent retention (P) with carapace width (CW, mm) is described by the following linear equation estimated by a weighted least-squares regression, i.e. the deviations of the predicted and measured data pairs (P, CW) were divided by the standard deviations of P from Fig. 4.7.2.1 (SAS Institute Inc. 1985).

$$P = 2.2432 \cdot CW - 2.7797 \quad (4.7.2.1)$$

The percent of males of different sizes retained for 24 h in Traps B-D was estimated by determining their ability to retain crabs relative to Trap A. Figure 4.7.2.2 shows size frequency distributions for catches by Traps A-D. Because both males and females were caught, the carapace widths for females were expressed as male-equivalent carapace widths for the same body lengths, using Eqns. 4.2.4 and 5 (page 28). Since retention is

determined largely by the ability of a crab to walk sideways out an escape port, the critical dimension in this regard is body length.

There were no apparent differences in retention of crabs among Traps A-D for crabs >155 mm CW, so the percent retained by Trap A is presumed to apply to Traps B-D. For Trap B, this presumption is apparently valid for crabs >145 mm CW. Carapace widths of 145 and 155 mm correspond to body lengths of 103 and 110 mm, respectively (from Eqn. 4.2.4, page 28). These body lengths are close to the escape port diameters for Traps B ( $\approx 103$  mm) and C-D ( $\approx 109$  mm), respectively (see Section 3.7.1), therefore the poorer retention of crabs smaller than 155 mm and 145 mm CW for Traps C-D, and Trap B, respectively, supports the contention that retention capabilities of traps are largely determined by escape port diameter.

For crabs smaller than 155 mm, for Traps C-D, and smaller than 145 mm, for Trap B, the percent retained in Traps B-D is determined by simultaneously and iteratively solving Eqn. 4.7.2.2 (below) for  $X_1$  of Traps B-D when the ratio of  $Q$  for Traps B-D relative to  $Q$  for Trap A, after a one day soak ( $T=1$ ), is determined from Table 4.7.2.1. The daily entry rate ( $U$ ) is assumed to be the same for all trap types, and  $X_1$  for Trap A is taken from Fig. 4.7.2.1. (See Ricker (1975) for the derivation of Eqn. 4.7.2.2 for an analogous problem).

$$Q = (U \div X_j) \cdot [1.0 - \exp(-X_j \cdot T)] \quad (4.7.2.2)$$

where:

- Q is the number of crabs in a trap after T days
- U is the daily entry rate of crabs into a trap
- X<sub>i</sub> is the -ln(daily probability of a crab in carapace interval i being retained by a trap)

Relative retention (ratio of Q's, Table 4.7.2.1) is determined by comparing the abundance of crabs in Traps B-D relative to Trap A. For example, the percent of males <145 mm CW retained in Trap B for 24 h is estimated as 0.220 times the percent determined for Trap A. Table 4.7.2.2 presents retention estimates for males 120-170+ mm CW for Traps A-D, expressed as probabilities. It is noteworthy in Fig. 4.7.2.2 that Trap C, with one 109 mm escape port, apparently retains smaller crabs more effectively than Trap B, with one 103 mm escape port, perhaps reflecting easier entry into Trap C through the larger escape port. One can presume that for Traps B-D the relative retention estimates are biased to some degree by small differences in entry rates, and perhaps also by agonistic interactions among crabs (see Section 4.7.3).

Table 4.7.2.1. The relative retention of crabs <155 mm CW, for Traps C-D, and crabs <145 mm CW, for Trap B, relative to Trap A. The relative retention for a trap type is the number of crabs caught by that trap type divided by the number caught by Trap A after equivalent one day soaks. For Trap A n=536 for crabs <155 mm CW, and n=322 for crabs <145 mm CW.

<u>Trap</u>	<u>n</u>	<u>Relative retention</u>	<u>Standard error</u>
B	71	0.220	0.023
C	164	0.306	0.020
D	87	0.162	0.016

Table 4.7.2.2. The probabilities of male C. magister being retained by Traps A-D for 24 h.

<u>Carapace width (mm)</u>	<u>Trap</u>			
	<u>A</u>	<u>B</u>	<u>C</u>	<u>D</u>
120-125	.130	<.001	<.001	<.001
125-130	.130	<.001	<.001	<.001
130-135	.192	<.001	<.001	<.001
135-140	.304	<.001	<.001	<.001
140-145	.416	<.001	.007	<.001
145-150	.529	.529	.012	<.001
150-155	.641	.641	.019	<.001
155-160	.753	.753	.753	.753
160-165	.866	.866	.866	.866
165-170	.978	.978	.978	.978
>170	.992	.992	.992	.992



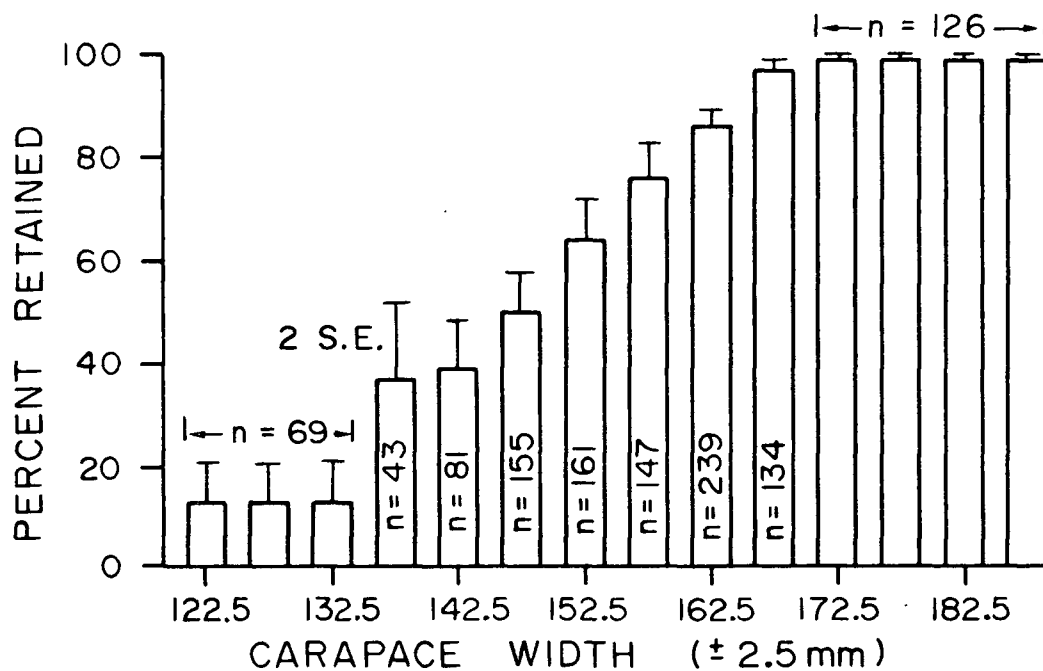


Figure 4.7.2.1. The percent of male *C. magister* retained by Trap A for 24 h, as a function of carapace width.

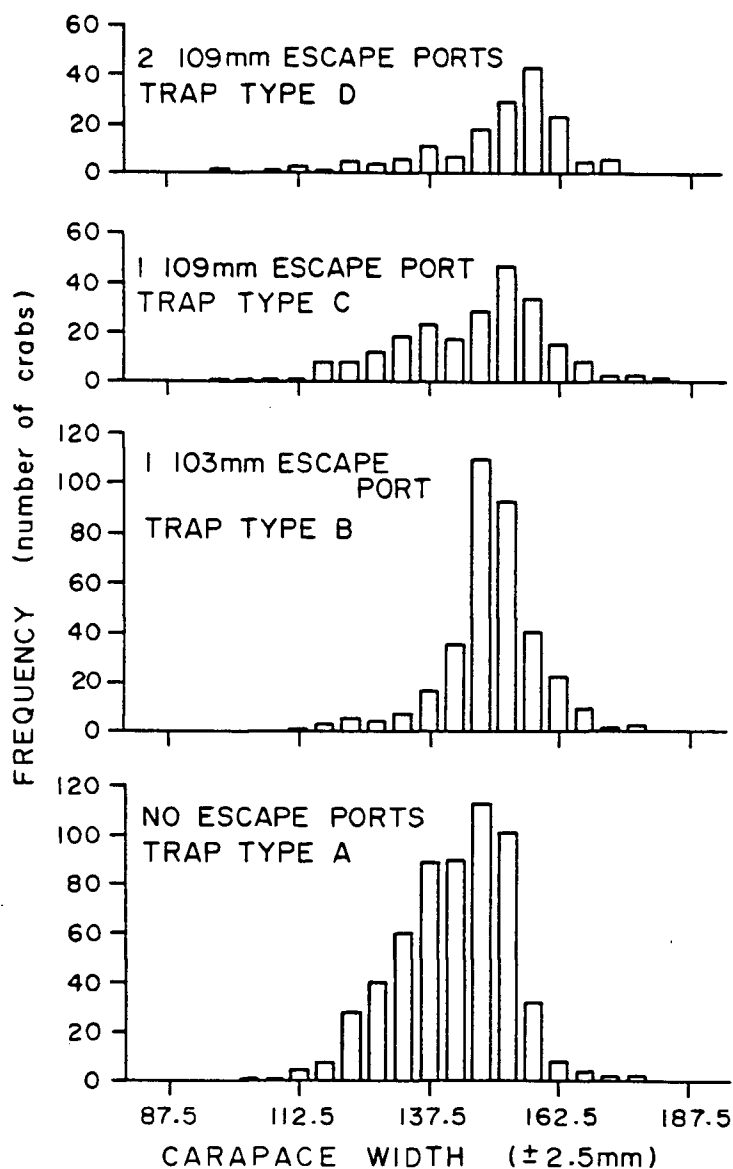


Figure 4.7.2.2. Size frequency distributions of *C. magister* caught in Traps A-D. Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.

#### 4.7.3 SOAK TIME AND BAIT EFFECTS

Previous workers have noted that crab traps saturate, i.e. attain a stable density of crabs after an adequate soak time as a result of a balance of entry and exit rates (Bennett 1974, Miller 1978, 1979, 1980). Also, from trapping experiments it was learned that as crabs became more abundant in traps the entry rate of crabs decreased. Experiments with C. productus and C. magister showed that traps hauled more often caught more crabs despite the bait not being changed for the duration of the experiment (Miller 1979). Miller (1978) observed that C. productus were less likely to enter traps already occupied by crabs. The experiments of Miller and Bennett, and the direct observations by Miller (1978) of C. productus behavior, indicated that crabs within traps competitively inhibited the entry of other crabs through agonistic encounters.

The soak time experiments were designed to emphasize the effect of C. magister individuals within a trap inhibiting the entry of more individuals. These agonistic encounters, when modified by differences in the ability of a trap to retain crabs of different sizes, produced different size frequency distributions for soak times of 1, 2, 5, 10 and 20 days. In Fig. 4.7.3.2 it can be seen how the smaller crabs, which entered the traps early, leave and are kept out presumably due to intimidation by larger crabs which become more abundant over time. It is possible that the reduction in the abundance of small crabs in traps over time is due to predation by larger

crabs, but there is no direct evidence of this. The bait-effectiveness experiments were designed to emphasize the decrease over time in the ability of bait to attract crabs. The results of changes in bait effectiveness were not as apparent as the soak time effects (see Fig. 4.7.3.6), particularly for smaller crabs, because of other dynamic interactions, e.g. agonistic interactions, size-dependent retention rates, and considerable variability in the data.

Although executed as two separate trapping experiments designed to emphasize agonistic interactions and changes in bait effectiveness over time for a single population, both experiments were influenced by both processes. Therefore, assuming no interaction between these processes, one would expect the parameter estimates for the equations describing these two processes to be the same for both experiments. Assuming this to be true, a dynamic model was developed to simulate the entry and exit of crabs within the combined set of traps used in each experiment. However, this assumption is not strictly true since Kolmogorov-Smirnov tests (Sokal and Rohlf 1981) indicated significantly ( $\alpha=.01$ ) different size frequency distributions between 24 h soaks of 16 traps in the bait effectiveness experiment and 20 traps in the soak time experiment, for both the 1985 and 1986 experiments (Fig. 4.7.3.1). Note that the magnitude of the differences are small ( $D=.20$  in 1985 and  $D=.13$  in 1986 experiments) and not unexpected considering the natural patchiness of animal distributions.

The dynamic model compared the predicted and observed densities and size frequency distributions within traps, the predicted number of crabs in any trap being a function of entry and exit rates, agonistic interactions and changes in bait effectiveness over time. In addition to the unknown parameters in the following equations describing agonistic behavior and changes in bait effectiveness, a vector of parameters represents the unmodified daily entry rates of crabs into a trap for each of twenty (in 1985) and eighteen (in 1986) 5 mm CW intervals between 90-200 mm CW. For any 5 mm CW interval this rate is defined as the number of crabs which would enter a trap each day if bait effectiveness did not decrease over time, and crabs within a trap have no effect on the entry rate of crabs. In practice this entry rate cannot be achieved for any soak time because bait deterioration and agonistic interactions begin as soon as a trap is placed in the water. Therefore, this vector is referred to as a vector of 'virtual entry rates'.

The general equation below (Eqn. 4.7.3.1) describes the net daily change in the number of crabs in a trap. Versions of this general equation presuming (1) no agonistic effects or changes in bait effectiveness over time, (2) agonistic effects alone, (3) changes in bait effectiveness alone, and (4) both of these processes operating, were applied to the data from both the 1985 and 1986 experiments. These variants of the dynamic model simulated the entry and exit of crabs into and out of traps for the duration of the soak time and bait-effectiveness experiments.

As mentioned above, the vector of virtual entry rates is an unknown, but the instantaneous exit rates ( $X_i$ ) for particular carapace width intervals ( $i$ ) are determined from the 24 h retention probabilities for Trap A from Table 4.7.2.2 (page 47). As further explained in Section 4.7.2, female carapace widths are converted to male-equivalent carapace widths for the same body lengths, since body length is the important body dimension determining a crabs ability to escape a trap.

$$dQ_i/dt = V_i \cdot R_1 \cdot R_2 - (X_i \cdot Q_i) \quad (4.7.3.1)$$

where:  $Q_i$  is the number of crabs in carapace interval  $i$  in a trap  
 $t$  is time the interval in days  
 $V_i$  is the daily virtual entry rate into a trap for a crab in carapace interval  $i$   
 $X_i$  is the  $-\ln(\text{daily probability of a crab in carapace interval } i \text{ being retained by a trap})$  from Table 4.7.2.2 (page 47)  
 $R_1$  the relative effect of agonistic interactions (from Eqn. 4.7.3.3)  
 $R_2$  the relative effect of changes in bait effectiveness (from Eqn. 4.7.3.5)

If one assumes that bait effectiveness does not change over time, and there are no agonistic interactions among crabs near traps, then  $R_1=1.0$  and  $R_2=1.0$ . Therefore, Eqn. 4.7.3.1 can be integrated from  $t=0$  to  $T$  to yield Eqn. 4.7.3.2 (see Ricker 1975, page 14, for an analogous derivation). Alternatively, these two variables vary from 0.0-1.0 decreasing the virtual entry rate ( $V_i$ ) as a result of agonistic interactions (Eqn. 4.7.3.3) and changes in bait effectiveness (Eqn. 4.7.3.5), respectively. When  $R_1 < 1$  or  $R_2 < 1$  then Eqn. 4.7.3.1 cannot be easily integrated, so

the entry and exit rates are integrated over time to predict the number of crabs in a trap at any time using the Runge-Kutta method of numerical integration (Boyce and DiPrima 1977).

$$Q_i = (V_i \div X_i) \cdot [1.0 - \exp(-X_i \cdot T)] \quad (4.7.3.2)$$

where:  $Q_i$  is the number of crabs in carapace interval  $i$  in a trap after  $T$  days  
 $V_i$  is the daily virtual entry rate into a trap for a crab in carapace interval  $i$   
 $X_i$  is the  $-\ln(\text{daily probability of a crab in carapace interval } i \text{ being retained by a trap})$  from Table 4.7.2.2 (page 47)

The equation used to describe the effectiveness of crabs within a trap reducing the virtual entry rate of crabs is introduced below. Equation 4.7.3.3 was formulated based on the results of competition experiments by Scrivener (1971) with the American lobster (Homarus americanus Milne-Edwards). He determined that even small differences in the relative sizes of two contesting individuals nearly assured the larger individual of winning the contest. For example, a legal-sized lobster with a carapace length 5% larger than its competitor won  $\approx 90\%$  of encounters, i.e. the loser backed away. The observations of Miller (1978) suggest similar behavior for C. productus.

Crab dry weight was used as a measure of a crab's competitive ability. Using weight presumes that competing individuals perceive a competitor's three-dimensional size, or a feature related to overall size, such as claw size (Scrivener 1971, Atema and Cobb 1980). In the special case of agonistic interactions between crabs within a trap and one attempting to

enter that trap, the weight of crabs within a trap is a proxy for the comparative competitive ability of a trap full of crabs. Although Eqn. 4.7.3.3 is likely an imperfect representation of relative competitiveness, other one and two parameter models based on numbers and/or weight as a measure of relative competitive ability were less capable of describing the data.

$$R_1 = \exp[-e \cdot (W + w_i)^f] \quad (4.7.3.3)$$

where:  $R_1$  is the relative entry rate into a trap for a crab of weight  $w$   
 $W$  is the total weight of crabs in a trap  
 $w_i$  is the weight of a crab in carapace interval  $i$  attempting to enter a trap  
 $e$  is the instantaneous rate of decrease in the entry rate of a crab as a function of the 'weight effect' ratio  $(W + w_i)$   
 $f$  allows the 'weight effect' ratio  $(W + w_i)$  to assume a nonlinear form

Dry weight ( $w$ , g) for males and females was determined from its relationship to carapace width (CW, mm) as defined by Stevens and Armstrong (1984) (Eqn. 4.7.3.4).

$$\ln(w) = -9.36 + 2.832 \cdot \ln(CW) \quad (4.7.3.4)$$

The equation chosen to describe changes in bait effectiveness over time is as follows. Equation 4.7.3.5 assumes a base rate at which crabs are attracted to traps in the absence of bait plus a complementary component which has a maximum ability to attract crabs at  $T=0$  and which declines exponentially with time.



$$R_2 = g + [(1.0 - g) \cdot \exp(-h \cdot T)] \quad (4.7.3.5)$$

where:

- $R_2$  is the relative entry rate of crabs into a trap
- $T$  is the age of the bait (in days)
- $g$  is the base relative entry rate of crabs into a trap when there is no bait
- $h$  is the daily instantaneous rate of decrease in bait effectiveness

Separate parameter estimates were obtained for the 1985 and 1986 experiments using the SIMPLEX nonlinear estimation package (Mittertreiner and Schnute 1985). A maximum likelihood objective function, the separation statistic 'A' of Schnute and Fournier (1980), was used to evaluate the parameter estimates. The Akaike information criterion (AIC) (Akaike 1974), which equals A plus twice the number of model parameters, was used to judge overall model performance, a lower value indicating a more suitable model.

Table 4.7.3.1 lists A and AIC for the four variants of the general model. In both 1985 and 1986 Model '4', which includes both bait-effectiveness and agonistic processes, outperformed all other models. For the 1985 experiments agonistic interactions were clearly dominant over changes in bait effectiveness. For both the 1985 and 1986 experiments the agonistic-interactions and bait-effectiveness equations explain considerable variability in the density and size frequency distribution of crabs among the experimental treatments. These satisfactory results suggest the structure of Eqns. 4.7.3.3 and 5 approximate the functional relationships for the dynamic processes they attempt to simulate.

The structure of the standardization model precluded estimation of confidence intervals for the parameter estimates of Eqns. 4.7.3.3 and 5, and the virtual entry rates. The application of approximate analytical techniques (Mittertreiner and Schnute 1985) was frustrated by problems with matrix inversion. Use of the bootstrap resampling method (Efron 1982), was prohibited by a lack of computer processing time.

---

Table 4.7.3.1. Comparison of different models explaining densities and size frequency distributions of C. magister in sets of traps which experienced different soak times and bait ages during equivalent experiments in 1985 and 1986. The objective function (A) is the separation statistic of Schnute and Fournier (1980). P is the number of parameters in the model. AIC (see text) measures model performance, the lower the value the more suitable the model.

---

<u>Model</u>	<u>1985</u>			<u>1986</u>		
	<u>A</u>	<u>P</u>	<u>AIC</u>	<u>A</u>	<u>P</u>	<u>AIC</u>
1. Constant entry rates <sup>a</sup>	657	20	697	736	18	772
2. Agonistic-interactions <sup>b</sup>	433	22	477	549	20	589
3. Bait-effectiveness <sup>c</sup>	601	22	645	545	20	585
4. 2 and 3 above <sup>d</sup>	422	24	470	469	22	513

---

<sup>a</sup> This model expects the same entry rate over time for each 5 mm CW interval. The number of crabs in a trap increases asymptotically (Eqn. 4.7.3.1 with  $R_1=1.0$  and  $R_2=1.0$ ).

<sup>b</sup> This model expects different entry rates and size frequency distributions over time (Eqns. 4.7.3.1 and 3,  $R_2=1.0$ ,  $R_1<1.0$ ).

<sup>c</sup> This model expects different entry rates and size frequency distributions over time (Eqns. 4.7.3.1 and 5,  $R_1=1.0$ ,  $R_2<1.0$ ).

<sup>d</sup> This model expects different entry rates and size frequency distributions over time (Eqns. 4.7.3.1, 3 and 5,  $R_1<1.0$  and  $R_2<1.0$ ).

---

Differences in the parameter estimates for the agonistic-interactions equation (Eqn. 4.7.3.3, Fig. 4.7.3.3) for the 1985 and 1986 experiments may reflect differences in the size frequency distributions of the crab populations for 1985 and 1986. Equation 4.7.3.3 cannot account for size-dependent biases in the relative competitiveness of C. magister individuals, so the higher density of smaller crabs in the 1985 experiments might be expected to produce parameter estimates different from those obtained for the 1986 experiments. Forty-four percent (44%) of the 1602 crabs captured in the 1985 experiments were <130 mm CW, compared to only 15% of the 2220 crabs captured in the 1986 experiments. As explained in Section 4.7.2, traps are ineffective in retaining crabs <135 mm CW. Thus, the difference in the parameter estimates for this model may also reflect poor estimates of crab retention probabilities for these crabs.

Different parameter estimates for the bait-effectiveness equation (Eqn. 4.7.3.5, Fig. 4.7.3.4) between 1985 and 1986 may be due to habitat differences. The 1985 experiments were performed in 12 m deep, calm water in upper Lemmens Inlet, whereas the 1986 experiments were performed in 8 m deep water with strong tidal currents near Indian Island. Bait effectiveness probably diminished less rapidly near Indian Island because of greater flushing of the bait and a more extensive odour trail. In contrast, in upper Lemmens Inlet, once the liquid content of the bait dissipated after a one or two day soak there was little current to produce an effective odour trail.

Further, the smaller crabs present in 1985 may have been attracted to traps as a refuge, thereby causing a high catch rate in the absence of bait.

Figure 4.7.3.5 presents response surface plots of the predicted numbers of crabs in each 5 mm CW interval within a 20 trap set as a function of soak time. The reduction in entry rates, and in the number of smaller crabs in the traps, over time is evident for both the 1985 and 1986 experiments. The virtual entry rate for any 5 mm CW interval is the slope, at time=zero, of the number of crabs as a function of time. The predicted and observed size frequency distributions for the 1, 2, 5, 10 and 20 day soak time trials are compared in Fig. 4.7.3.2.

Figure 4.7.3.6 presents response surface plots comparing the predicted and observed numbers of crabs in each 5 mm CW interval within a 16 trap set representing bait ages (at the time bait is placed in a trap) from zero to eight days. The observed size frequency distribution for the ninth day was obtained with no bait in the traps. The decrease in bait effectiveness over time, as shown in Fig. 4.7.3.4, does not appear as dramatically in Fig. 4.7.3.6 because of the confounding effects of agonistic interactions and escapement.

Residuals are not randomly distributed above and below the plane of the response surface in Figs. 4.7.3.2 and 6. There are several possible reasons. It may (1) reflect poor estimates of crab retention probabilities for particular carapace width

intervals, (2) reflect the influence of tides, currents or other interventions, (3) indicate imperfect understanding of agonistic-interactions and bait-effectiveness processes, and (4) indicate the presence of unidentified processes. In particular, the theoretical suitability of the agonistic-interactions equation is difficult to evaluate since little is known about the dynamics of such interactions.

The size frequency distributions, and abundance of legal-sized males, were more typical of commercial traps in the Indian Island experiments than in the upper Lemmens Inlet experiments. Thus, the 1986 experiments were considered to provide better parameter estimates for the equations modeling the dynamic interactions between crabs and commercial traps. Although the general model including both the agonistic-interactions and changes in bait effectiveness equations is imperfect, the 1986 parameter estimates for this model were used when standardizing commercial samples to reduce bias introduced by different soak times and trap types.

Another result of different soak times was different proportions of hard- and soft-shelled crabs within traps. Legal-sized males are soft-shelled for the first few months following a moult (see Table 4.10.1, page 80), and during this period they enter traps, but are vulnerable in contests with hard crabs. Figure 4.7.3.7 suggests soft-shelled crabs may not readily enter or survive in traps containing hard-shelled crabs.

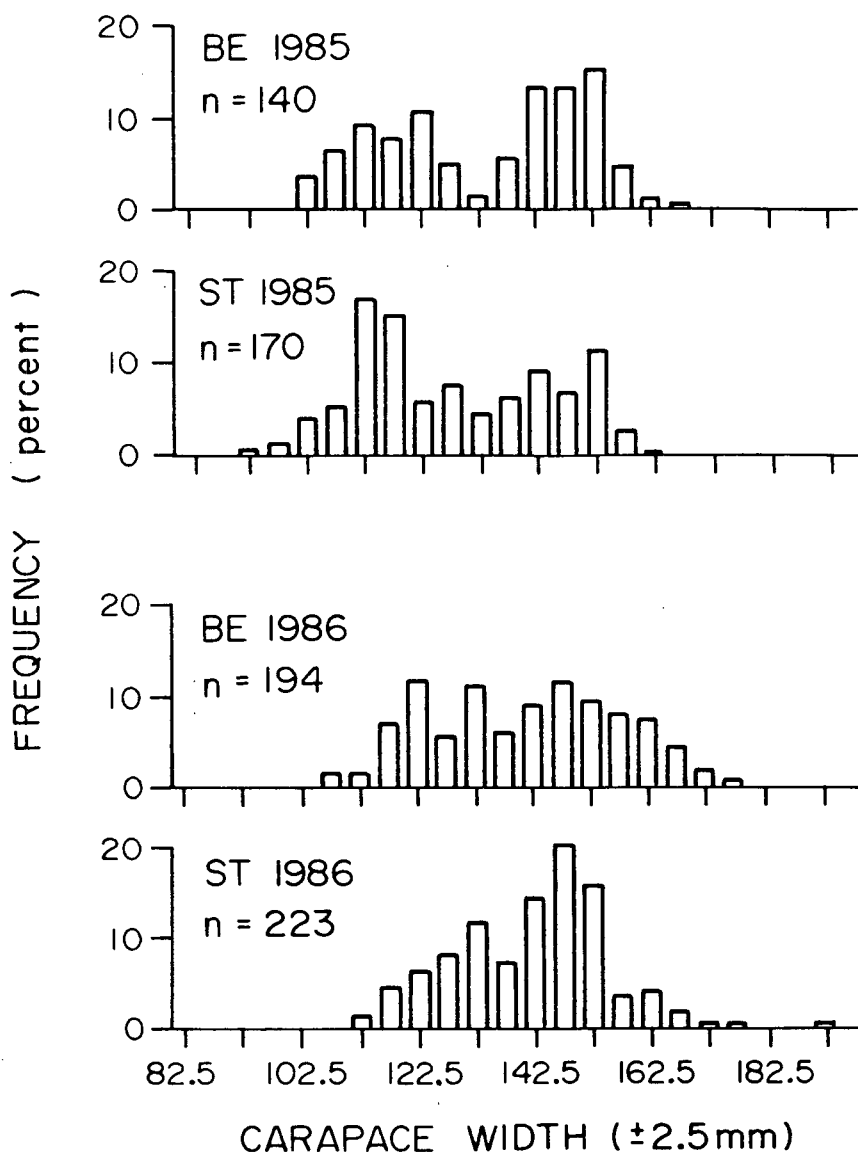


Figure 4.7.3.1. Comparison of size frequency distributions of *C. magister* in traps soaked 24 h in the soak time (ST, 20 traps) and bait effectiveness (BE, 16 traps) experiments in 1985 and 1986. Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.

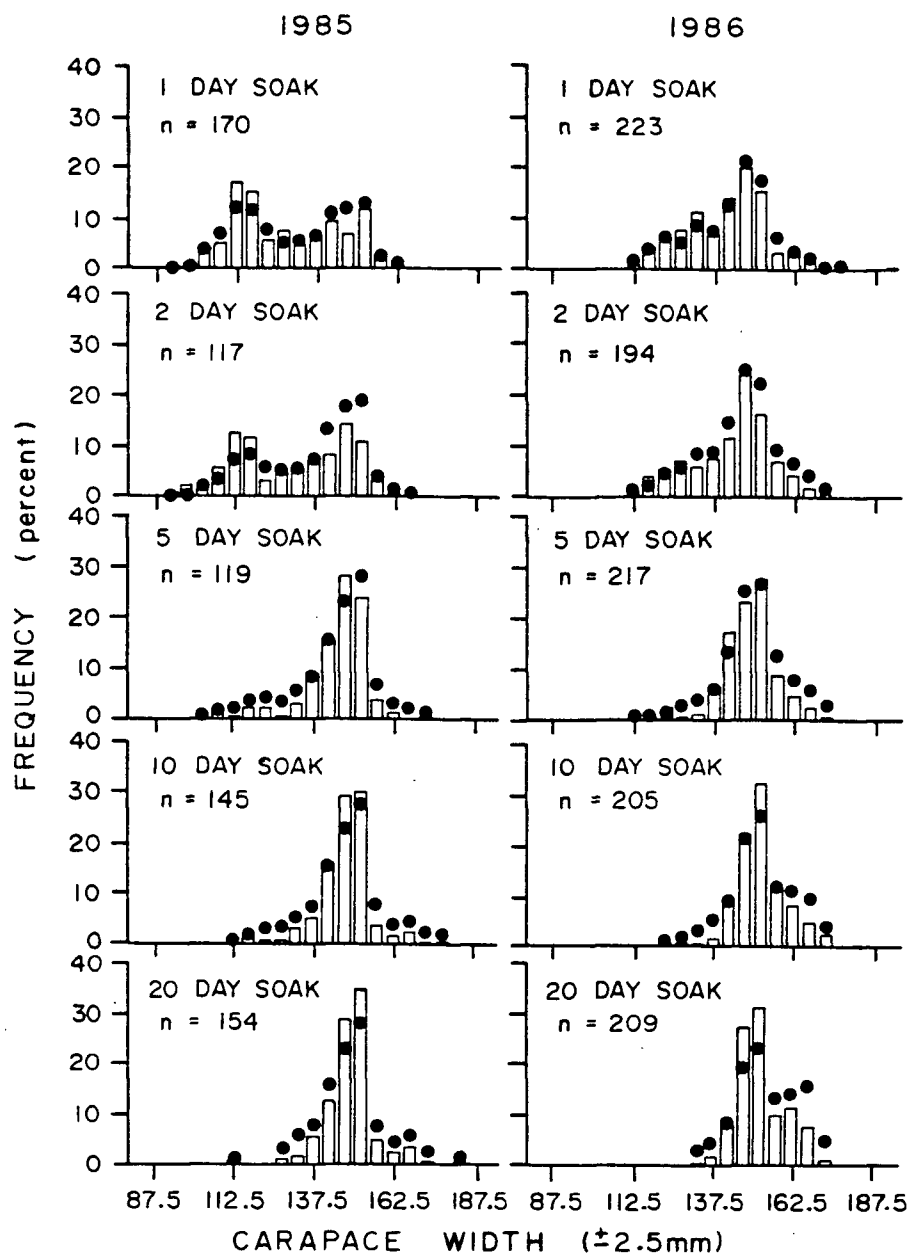
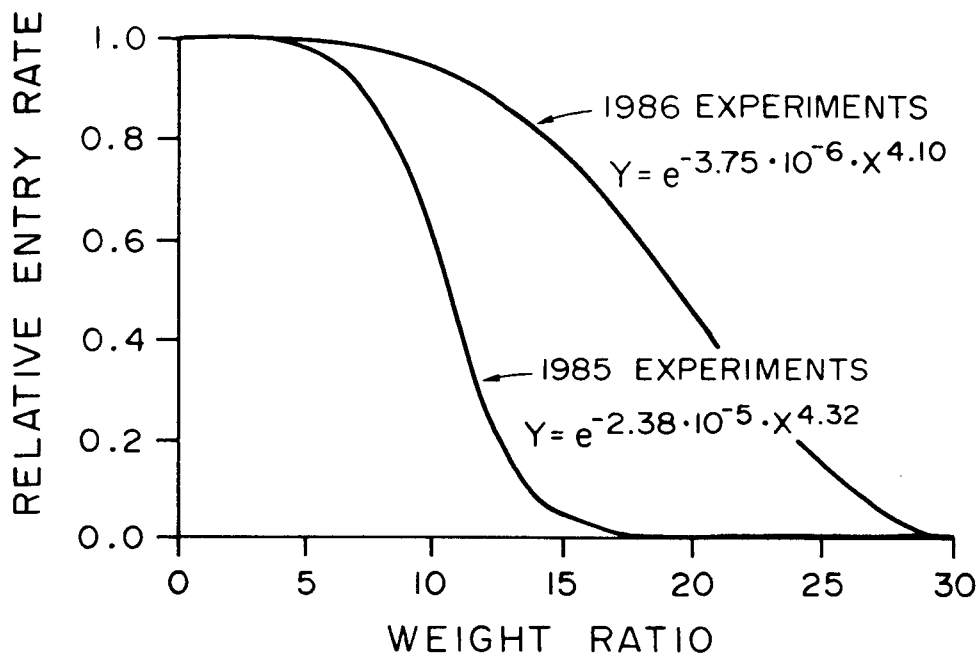


Figure 4.7.3.2. Size frequency distributions of *C. magister* for sets of 20 type A traps with different soak times from equivalent experiments in 1985 and 1986. Solid circles profile predicted size frequency distributions using Model '4' (Table 4.7.3.1). Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.




---

Figure 4.7.3.3. The relative rate at which C. magister enter Trap A, as a function of the ratio between the weight of crabs in a trap, and the weight of the crab attempting to enter the trap. This plot uses the best parameter estimates for Eqn. 4.7.3.3 from Model '4' (Table 4.7.3.1).

---



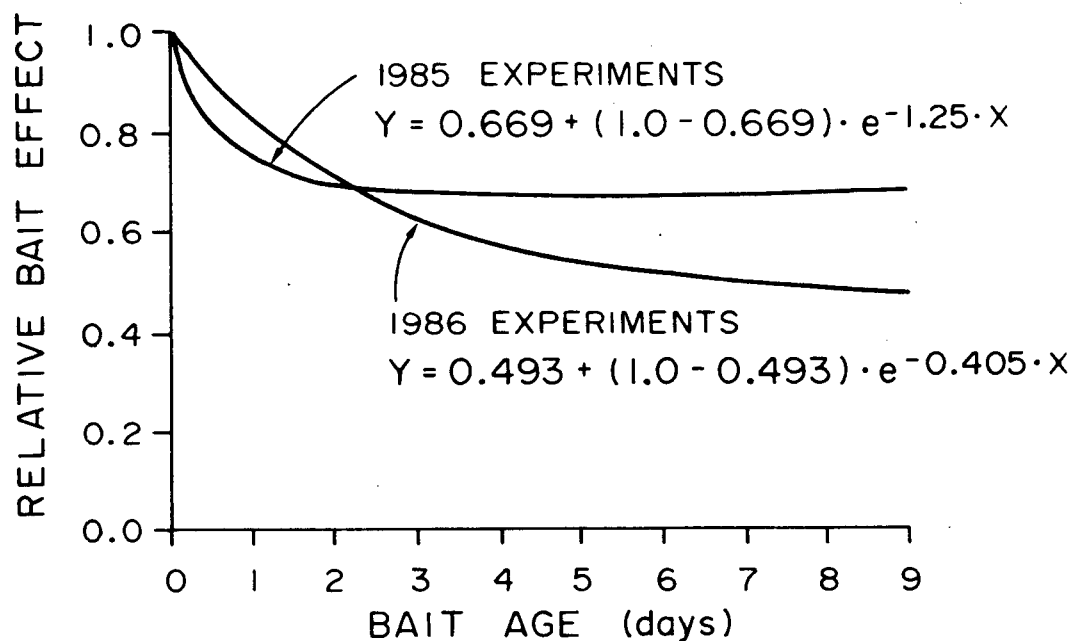


Figure 4.7.3.4. The relative entry rate of C. magister into Trap A as a function of bait age. This plot uses the best parameter estimates for Eqn. 4.7.3.5 from Model '4' (Table 4.7.3.1).

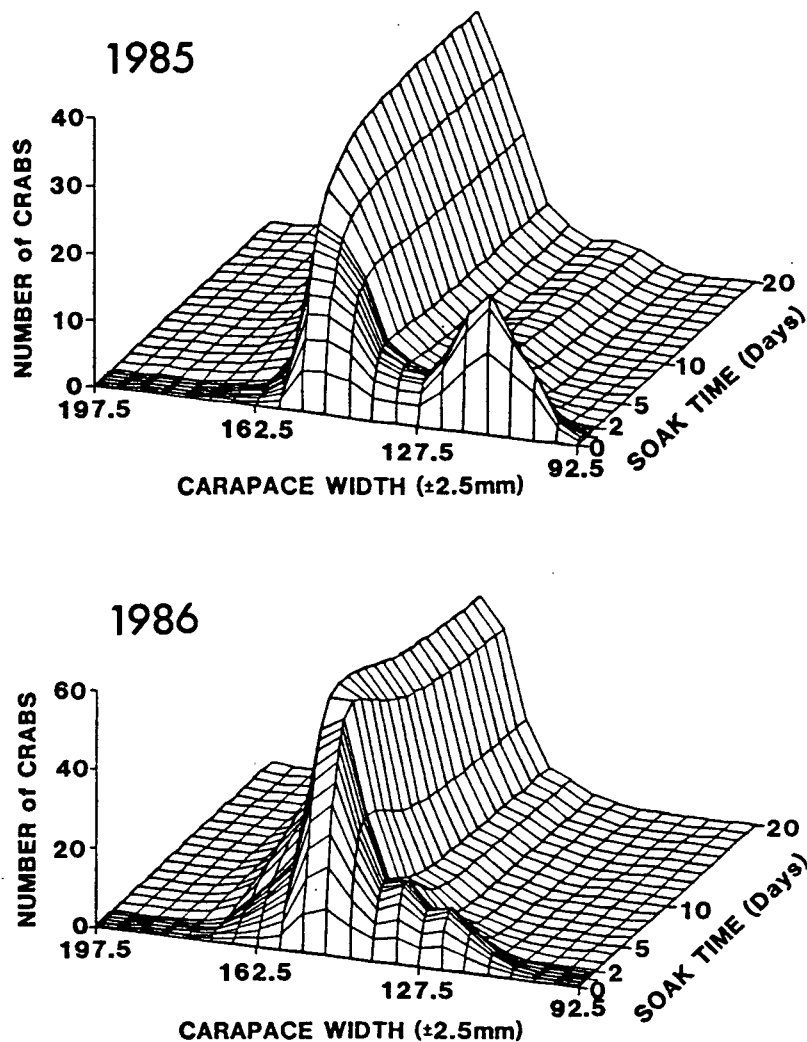


Figure 4.7.3.5. Response surface of the predicted changes in the size frequency distribution of *C. magister* within 20 type A traps, as a function of time. These results use the best parameter estimates for Eqns. 4.7.3.3 and 5 from Model '4' (Table 4.7.3.1). Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.

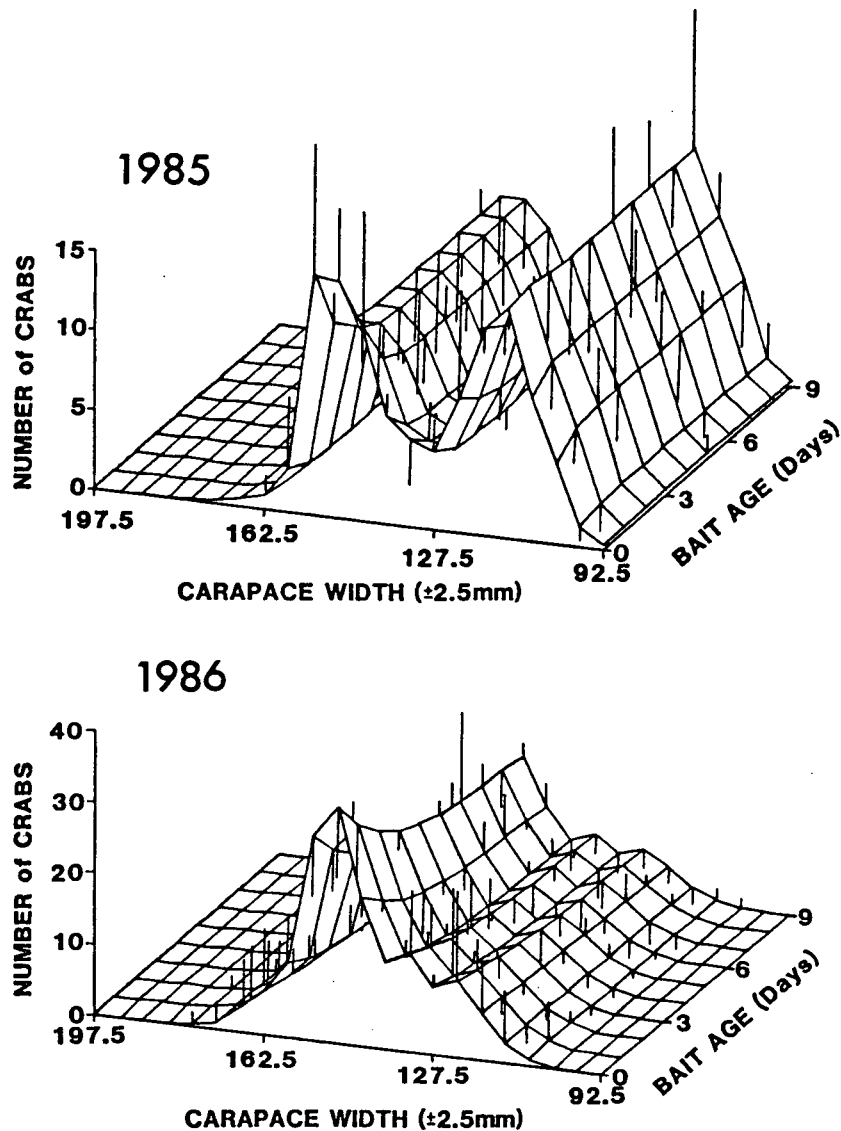
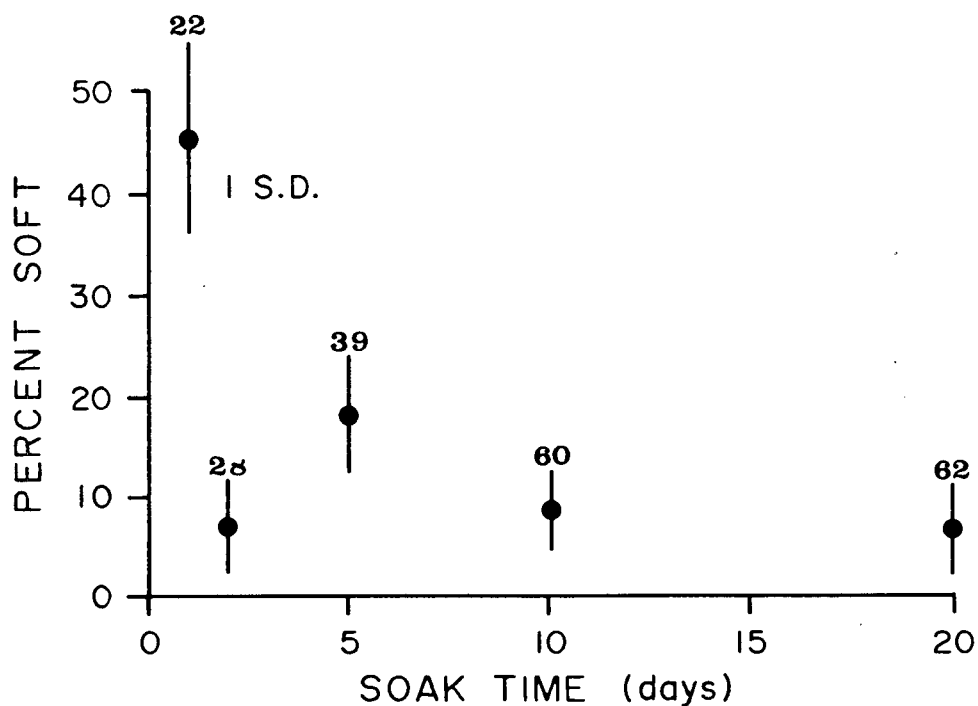


Figure 4.7.3.6. Response surface of the predicted size frequency distributions of *C. magister* within 10 sets of 16 type A traps. Each set used bait ranging in age from zero to eight days, soaked for one day. The bait was removed for the ninth day. The vertical lines show the observed data for a particular combination of bait age and carapace width, for differences greater than one. These results use the best parameter estimates for Eqns. 4.7.3.3 and 5 from Model '4' (Table 4.7.3.1). Female carapace widths are expressed as male-equivalent carapace widths for the same body lengths.



---

Figure 4.7.3.7. The percent of soft-shelled legal-sized male *C. magister* in Trap A, as a function of soak time. These results were obtained from the soak time experiment performed near Indian Island (H; Fig. 2.1, page 9) in 1986. Above the S.D. bars is the number of legal-sized males caught in 20 traps.

---

#### 4.8 TRAP DISTRIBUTION

Figure 4.8.1b presents time series profiles for the number of traps fished at specific sites throughout the main study area. Figure 4.8.1a compares the number of traps fished in Lemmens Inlet as determined (1) by counting the trap buoys and, (2) from interviews with the fishermen. The similarity of the assessments suggests the time series profiles in Fig. 4.8.1b are an accurate documentation of trap distributions.

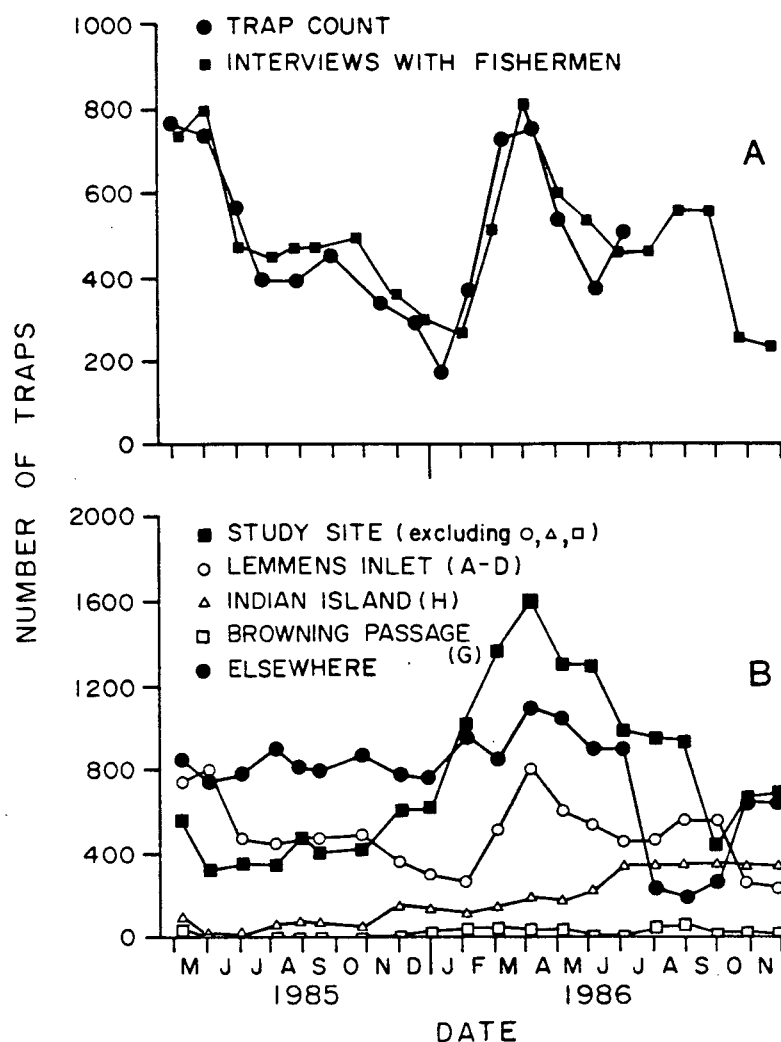


Figure 4.8.1. (A) Time series comparison of the number of trap buoys counted in Lemmens Inlet, and the number of traps estimated by interviewing fishermen. (B) Time series of the number of traps estimated by interviewing fishermen. The 'Elsewhere' category includes traps fished outside the study area in Statistical Area 24 by fishermen who also fish in the study area. The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).

#### 4.9 COMMERCIAL EXPLOITATION OF MALES

I define the degree of exploitation of legal-sized males as the proportion of males missing from the  $155.0 \pm 11.2$  mm instar. This proportion was estimated using a size frequency analysis which measured the proportion of males missing from the 155.0 mm instar, as described diagrammatically in Fig. 4.9.1. The influence of the 183.8 mm instar is unimportant because of low survivorship to this instar (Section 4.13). As evident in Fig. 4.9.1, there is little overlap between the 155.0 mm and the next smaller  $128.0 \pm 10.5$  mm instar, with the 155.0 mm instar remaining relatively distinct even when considerably lower in abundance than the 128.0 mm instar. Nevertheless, to reduce the influence of smaller instars, whose abundance is less confidently measured, the size frequency analyses were performed on a subset of the distributions  $>145$  mm CW. Since males continually moult into this instar, which I define by size and not by cohort, the proportion exploited measures the difference between recruitment and exploitation.

Before performing the size frequency analyses measuring exploitation of the 155.0 mm instar, the size frequency distributions were standardized to minimize bias introduced by different soak times. This was done using the results from the model which analyzed the soak time and bait-effectiveness experiments (Section 4.7.3). The parameter estimates for Eqns. 4.7.3.3 and 5 (pages 55 and 56) obtained for the 1986 experiments near Indian Island were used. The unknown parameters are the

'virtual entry rates' for each 5 mm CW interval. The vector of crab retention probabilities (for each 5 mm CW interval) appropriate for each trap type (Table 4.7.2.2, page 47) was used to estimate the escapement of crabs from traps. The standardization model simulated the entry and exit of crabs into the set of traps comprising the commercial sample. The accepted estimates for the vector of virtual entry rates were those which yielded the size frequency distribution, after the appropriate soak time, which most closely resembled that of the commercial sample. As in the analysis of the soak time and bait effectiveness experiments, the separation statistic 'A' of Schnute and Fournier (1980), was used to evaluate the parameter estimates.

Figure 4.9.2 plots the percent of legal-sized male C. magister taken by the fishery for dates from April 1985 until August 1986. Exploitation increased rapidly in spring 1985 and remained at 60-90%. In upper Lemmens Inlet, a poorer crab habitat, exploitation was near 100%. This rapid increase in exploitation suggests harvesting of a previously unavailable 155.0 mm instar abundant in 1985 and 1986. The number of traps increased steadily until summer 1986 (Fig. 4.8.1b, page 69) in response to fishing success.

If the 1985 and 1986 155.0 mm instars were indeed more abundant than in the immediately preceding years, one would expect an increase in abundance of sublegal-sized males in the 155.0 mm instar over this period. Figure 4.9.3 shows that the



virtual entry rates for males 145-155 mm CW approximately doubled. Because of high natural mortality (Section 4.13), the recruitment rate over this period was probably much greater, suggesting there may have been larval settlement in this area in 1982 and 1983, but not in 1981.

Figure 4.9.4 shows that fishing success (the number of legal-sized males caught per 100 traps per soak day) in Lemmens Inlet increased during spring and summer and was poor in winter. Outside Lemmens Inlet fishing success remained relatively constant throughout the year. The pattern observed in Lemmens Inlet probably reflects relative abundance since exploitation rates there were high, i.e. a high trap density (Fig. 4.8.1, page 69) and short (1-2 days) soak times. A similar seasonal pattern of abundance is suggested by the standardized data in Fig. 4.9.5. In contrast, the absence of a seasonal pattern similar to that observed in Lemmens Inlet (Fig. 4.9.4) outside of Lemmens Inlet is probably due to the relationship between abundance and catch rate being disguised by lower effort, i.e. a lower trap density (Fig. 4.8.1) and longer (often at least a week) soak times.

For reasons explained above, the high catch rate near Indian Island in spring 1986 is thought to result from recruitment to the fishery of the 1983 year-class which may have settled on adjacent mudflats. Effort increased near Indian Island about this time (Fig. 4.8.1b, page 69) in response to the increased catch rate.

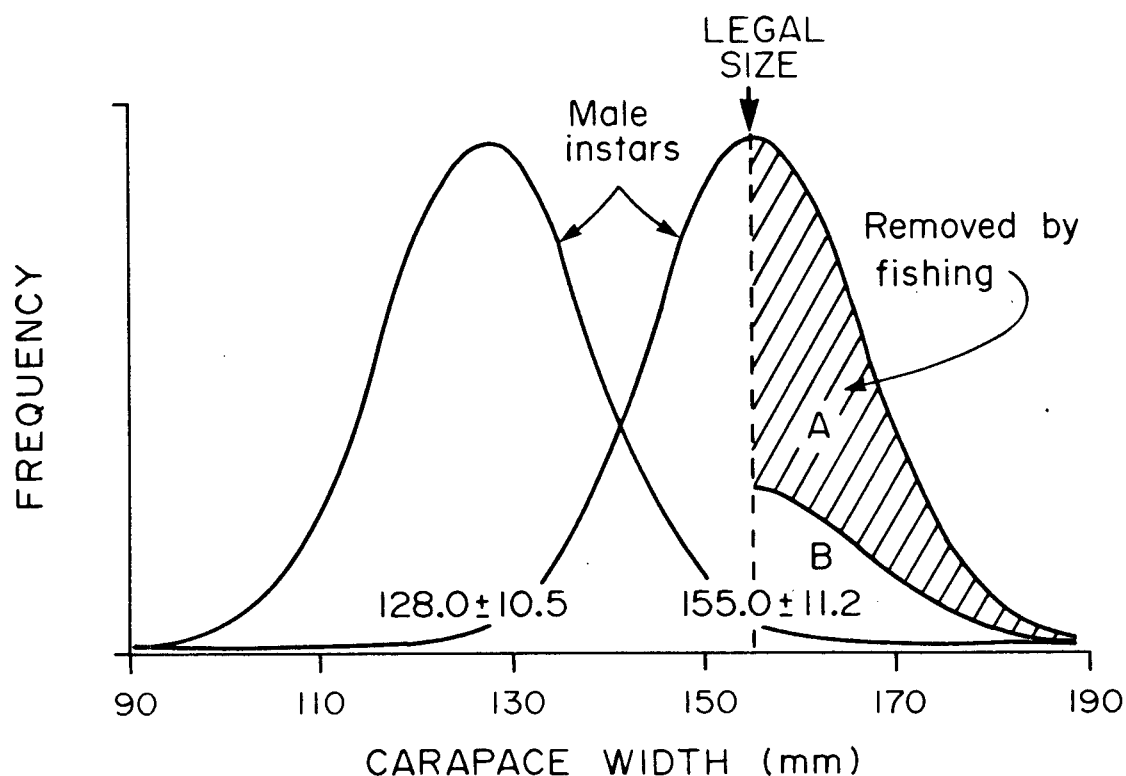


Figure 4.9.1. Diagram explaining how the degree of exploitation of male *C. magister* in the  $155.0 \pm 11.2$  mm instar was estimated. The proportion exploited ( $A/[A+B]$ ) was determined by size frequency analysis.

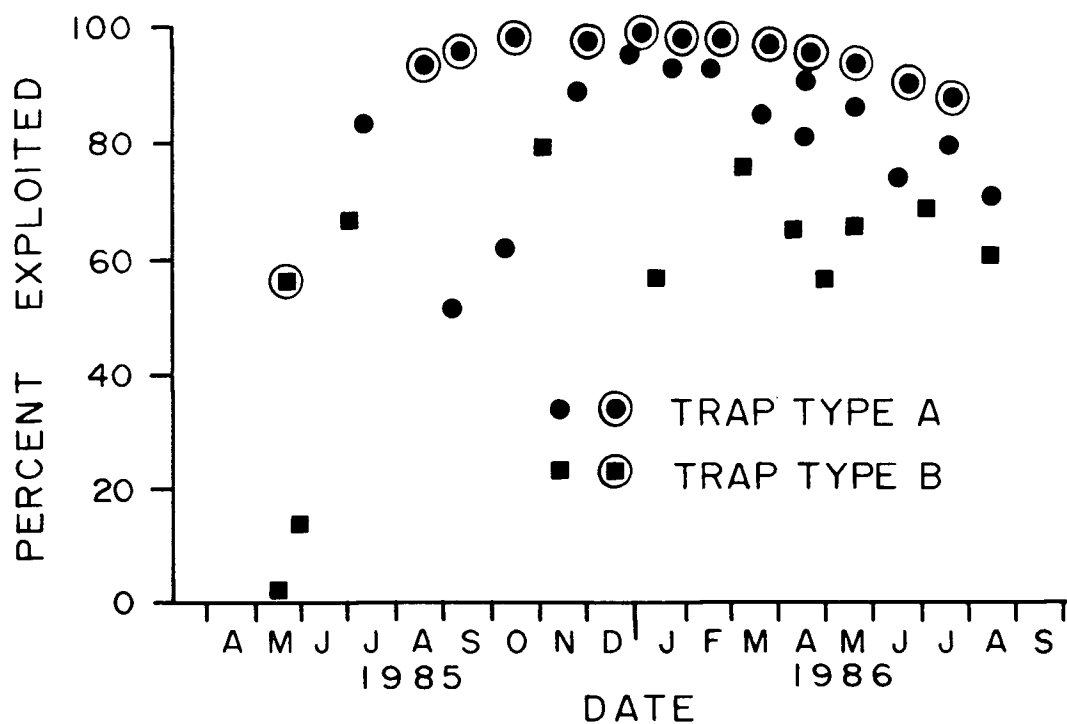


Figure 4.9.2. The percent of legal-sized male C. magister removed from the 155.0 mm instar by fishing, as determined by size frequency analysis of trap samples. The encircled data points are for upper Lemmens Inlet. The remainder are for the rest of the study area.

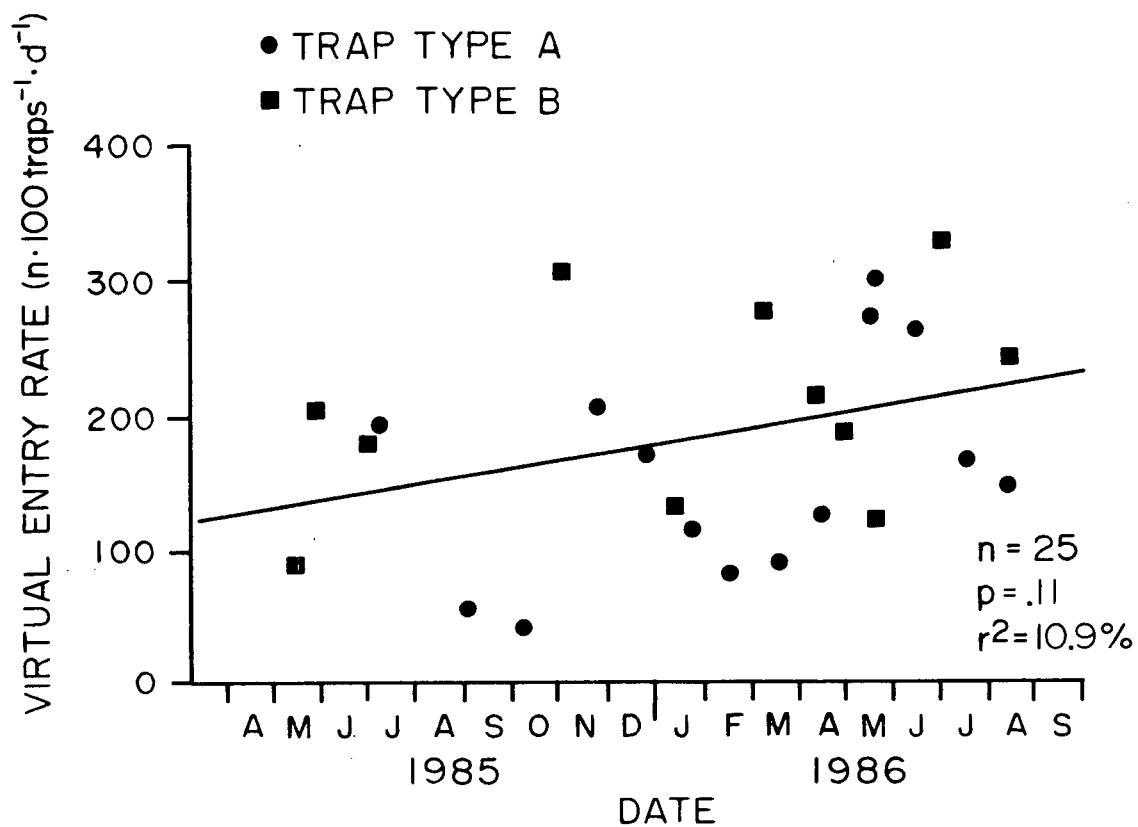


Figure 4.9.3. Linear regression of virtual entry rates of male C. magister 145-155 mm CW into traps over time. Data from upper Lemmens Inlet, a poor crab habitat, are not included in this plot.

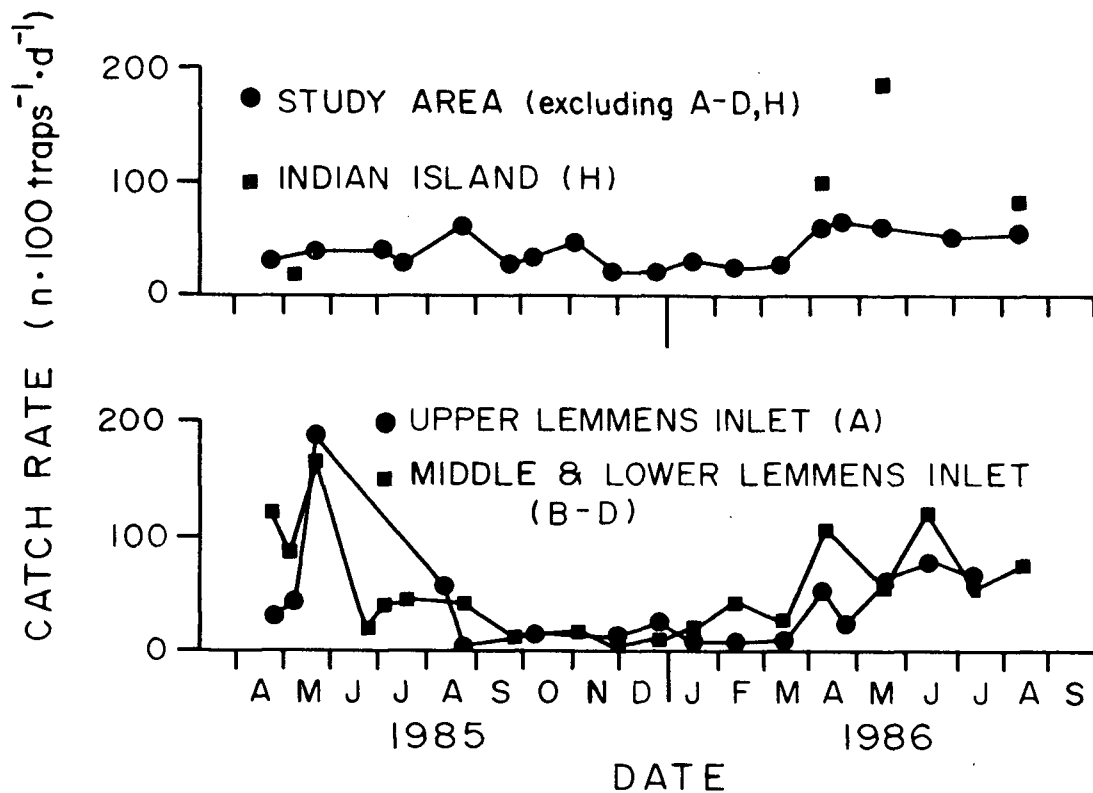


Figure 4.9.4. Time series of commercial catch rates of legal-sized male *C. magister*. The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).

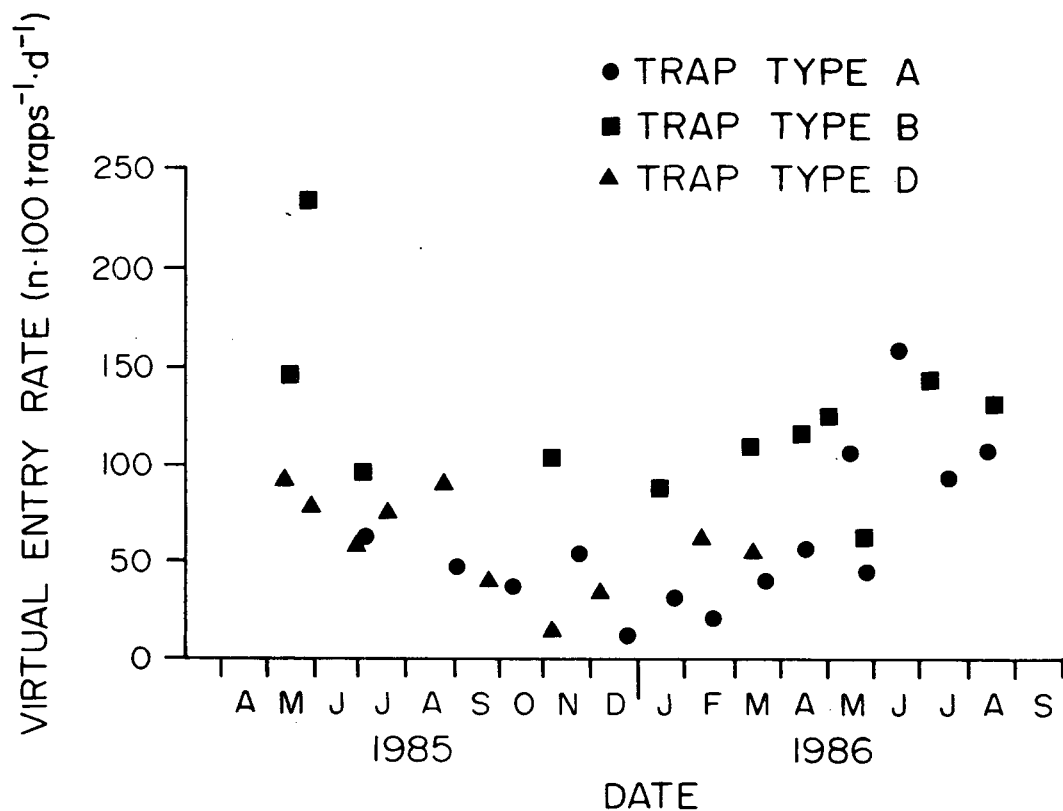


Figure 4.9.5. Virtual entry rates of legal-sized male *C. magister* into traps over time. Data from upper Lemmens Inlet, a poor crab habitat, are not included in this plot.

#### 4.10 MALE MATING ACTIVITY

Figure 4.10.1 profiles the percent occurrence of mating marks (Butler 1960) on the claws of males for 5 mm intervals ranging from 120-190 mm CW. Mating marks are caused by a male embracing a female and indicate involvement in mating. They occur with increasing frequency above  $\approx 120$  mm CW as males approach legal size, then less frequently for legal-sized males. Note that because the samples include males collected after different periods of time in an instar, the percent of males with mating marks is not a measure of the number of males in a particular carapace width interval that will eventually mate. The distribution of mating activity for carapace width intervals below legal size approximates the normal distribution of the  $155.0 \pm 11.2$  mm instar (see Fig. 4.9.1, page 73). Since males in larger instars are rare (Section 4.13), the mating marks are predominately on males in the 155.0 mm instar, suggesting that this instar is responsible for most mating activity.

Figure 4.10.2 compares the relative mating activity of sublegal- and legal-sized males from July 1985 until August 1986. Since mating marks occur infrequently on males  $< 140$  mm CW, the sublegal category includes males 140-154 mm CW. To compare the mating activity of legal- and sublegal-sized males, a time series of mating ratios was obtained by dividing the percent occurrence of mating marks on sublegal-sized males by their percent occurrence on legal-sized males. An intervention model (Noakes 1986), using the McLeod-Hipel algorithm (Hipel and McLeod 1987),

revealed no significant autocorrelations in the time series when comparing 1985 and 1986 mating ratios (Fig. 4.10.3). Therefore, a student's T-test (Sokal and Rohlf 1981) was used to conclude that the mean ratio for 1986 was  $\approx 29\%$  ( $p < .001$ ) of the 1985 ratio.

This suggests lower mating activity by legal-sized males in 1986, when effort (Fig. 4.8.1b, page 69) and exploitation (Fig. 4.9.2, page 74) were higher. A high exploitation rate means most males caught are soft-shelled. With  $F=5.11-6.90$  and  $M=3.48-4.48$  (from Section 4.13), only 6-12% of legal-sized males survive 90 days, near the time needed for their shell to harden before they can mate (Table 4.10.1). This analysis corroborates Fig. 4.10.2 which shows that mating marks generally occurred on  $<10\%$  of legal-sized males in 1986. Covariation of the time series for mating marks and hardness is evident Fig. 4.10.2. The implication is that exploitation rates can be high enough to markedly reduce the opportunity for legal-sized males to mate.

The high ratio of mating activity in May 1986 (Fig. 4.10.3) is not typical for the study area, so was not included when comparing 1985 and 1986. Most of these crabs were hard-shelled, and from their shell condition, had not moulted recently. These crabs, with an estimated age of at least four years, briefly appeared in shallow water near the open coast (F; Fig. 2.1, page 9), possibly from nearby deeper, more sheltered, habitat where they wintered. They do not reflect the moulting and mating activity of the local shallow water population. Similar movement was observed for small (first-year) crabs (Section 4.11).



---

Table 4.10.1. The percent of male C. magister, tagged when soft-shelled, which were hard-shelled when recovered. The results are reported for 30 day intervals of time-at-large. The carapace widths of recovered males were approximately normally distributed ( $153.4 \pm 6.0$  mm) and ranged from 135-173 mm.

---

<u>Time-at-large (d)</u>	<u>Sample size</u>	<u>Percent hard-shelled</u>
1-30	31	$32.3 \pm 8.4^a$
31-60	20	$60.0 \pm 11.0$
61-90	23	$91.3 \pm 5.9$
>90	56	100.0

---

<sup>a</sup> 1 S.E. of the estimate.

---

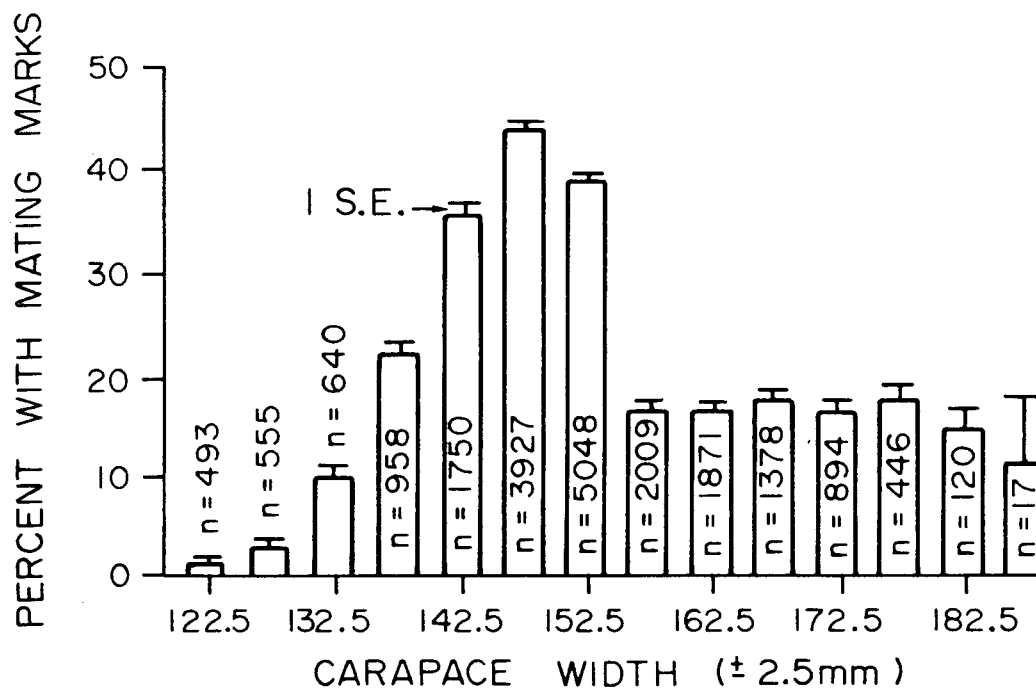


Figure 4.10.1. The percent of male C. magister with mating marks (Butler 1960) as a function of carapace width. The minimum legal size limit is  $\approx 154$  mm CW.

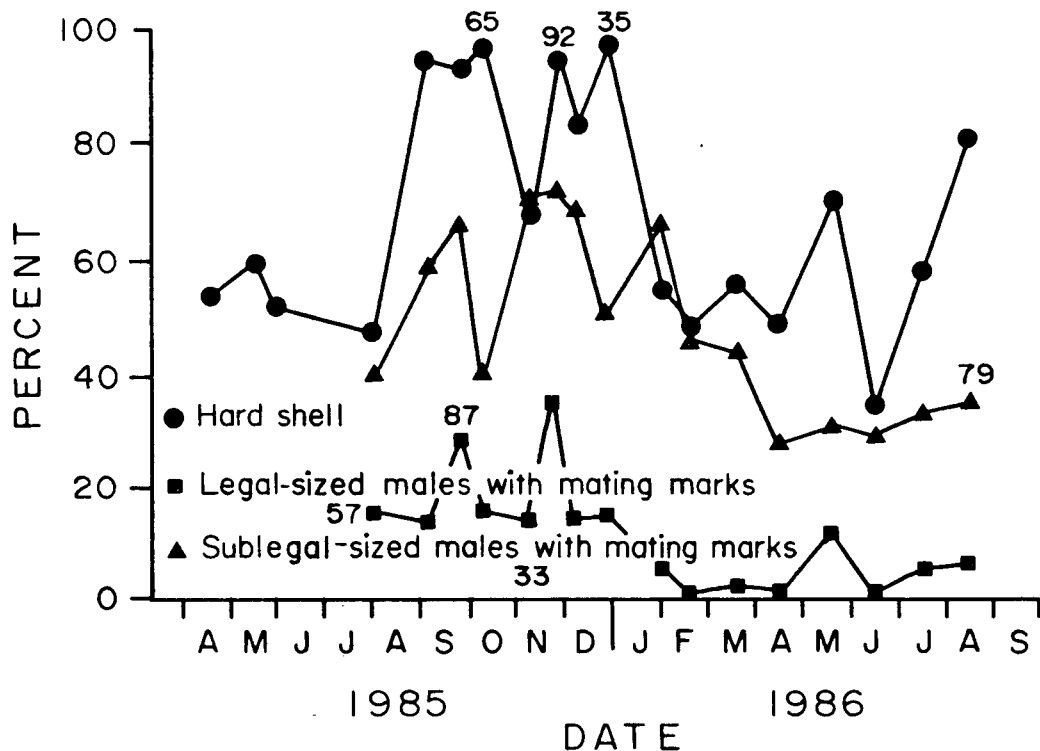


Figure 4.10.2. Time series of the percent of hard-shelled legal-sized (>154 mm CW) male, legal-sized male with mating marks (Butler 1960), and sublegal-sized (140-154 mm CW) male *C. magister* with mating marks. Except where noted, all sample sizes are >100 crabs.

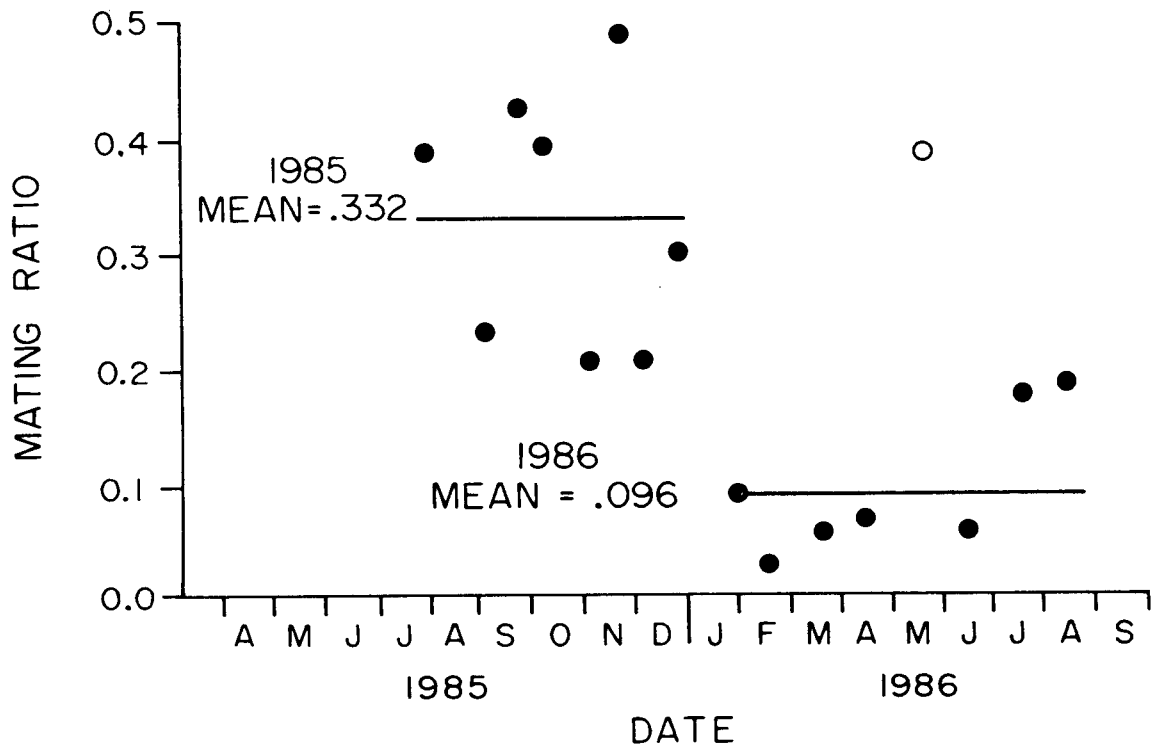


Figure 4.10.3. Time series indicating that the relative level of mating activity by legal-sized male C. magister in 1986 was  $\approx 29\%$  of the level in 1985. The sublegal:legal mating ratio is obtained by dividing the percent of legal-sized males with mating marks by the percent of sublegal-sized males with mating marks. The ratio for May 1986 was excluded from the comparison for reasons given in the text.

#### 4.11 SPATIAL AND TEMPORAL DISTRIBUTIONS

Beam trawl surveys in 1985 and 1986 collected few small C. magister except in the selected locations considered below. In 46 beam trawl samples, one year old ( $\approx 40-75$  mm CW) and two year old ( $\approx 75-145$  mm CW) crabs (Butler 1961, Stevens and Armstrong 1984) were found at densities generally less than  $10 \text{ ind} \cdot \text{ha}^{-1}$ . Where higher densities were found, there were important seasonal differences, and differences in the relative proportions of males and females. Note that beam trawls are not 100% efficient, so reported densities are only an index of abundance.

A peak in abundance of male and female one year old crabs on the shallow sand bottom of an exposed shore occurred in summer 1985 (Fig. 4.11.1b). Their occurrence is suspected to be the result of movement into shallower water (E; Fig. 2.1, page 9) of the 1984 year-class which settled on the outer coast. Abundance declined quickly, but some may have moved to the entrance of Lemmens Inlet by December 1985 (Fig. 4.11.1a). Similar movement of larger crabs into shallow water is described in Section 4.10.

In upper Lemmens Inlet the densities of two year old males and females were initially low in summer 1985 and declined through 1986 (Fig. 4.11.2a). This cohort was abundant elsewhere suggesting upper Lemmens Inlet is poor crab habitat.

The highest density of males was observed in middle Lemmens Inlet (Fig. 4.11.2b). During autumn 1985 and the subsequent winter, male densities steadily increased to  $>1200 \text{ ind} \cdot \text{ha}^{-1}$ .

Toward the mouth of Lemmens Inlet male densities generally declined (Fig. 4.11.2c,d). Because densities of two to three year old males elsewhere were consistently low, the increase in the number of males in middle Lemmens Inlet could be due to movement away from exposed shallow water during winter. They may have concentrated in middle Lemmens Inlet because of poor habitat further up the inlet.

The high density of males in middle Lemmens Inlet decreased rapidly during late spring 1986. Most males were in the 128.0 mm instar (Table 4.6.3, page 41) and moulted to legal size in 1986, after which they were soon caught in an intense fishery. Figure 4.8.1b (page 69) suggests that 25-35% of the fishing effort in the study area was concentrated in Lemmens Inlet during spring 1986. Males began to enter the fishery about three years after larval settlement (in spring 1986), and continued to moult to legal size for the next 6-9 months (see Fig. 4.13.3, page 105).

A high density of two year old females was observed in the narrow channel at the lower end of Lemmens Inlet in June 1985 (Fig. 4.11.2c). Density declined after this date, but increased during autumn in the entrance to Lemmens Inlet (Fig. 4.11.2d) 0.5-1.0 km seaward of the narrow channel. Female density further up Lemmens Inlet continued to decline suggesting seaward movement. The increase in female abundance in September 1986 where the main channel out of the study area meets the open coast

(Fig. 4.11.1c) also suggests seaward movement of females. These females were three years old and were mainly in the 135.5 and 149.4 mm instars (Table 4.6.4, page 42).

Despite the high density of females in the channel at the mouth of Lemmens Inlet during summer 1985 (Fig. 4.11.2c) it appears that all females that moulted to the next instar were mated (Fig. 4.3.1, page 29). Most of the data for the smaller females in Fig. 4.3.1, which documents the percent of females inseminated as a function of carapace width, were obtained from crabs collected near this location.

The relative abundance of larger females in the study area was assessed by trap sampling. Females were most abundant in spring (Fig. 4.11.3) perhaps because they forage more actively after a winter of incubating eggs. The highest observed abundance of females in spring 1985 and 1986 was in the main channel out of the study area (Table 4.11.1) where the high abundances of the 135.5 and 149.4 mm instars were collected in beam trawls in September 1986. Table 4.11.1 reports on females >145 mm CW mainly representing instars four and five years old. Females this size have a high mortality rate ( $M > 2.0$ , Hankin et al. 1985), so the lower catch rates in 1986 may indicate a weak 1981 year-class, as interpreted from Fig. 4.9.3 (page 75).

The relatively high densities of male and female C. magister collected in beam trawl samples near Indian Island (Table 4.11.2) may have resulted from a larval settlement on nearby mudflats in

1983. In contrast to Lemmens Inlet, near Indian Island male density decreased relative to female density from 1985 to 1986. Females may prefer an open coast habitat, but deep water surrounding Indian Island may prevent easy access to Browning Passage, thereby confining them to the Indian Island area.

Tables 4.11.3 and 4 summarize tag releases and recoveries of male and female C. magister, respectively. Most male and female recoveries occurred near where they were tagged. The only suggestion of directional movement is the large number of recoveries of males, tagged in the poor habitat of upper Lemmens Inlet, lower down the inlet. However, this probably also results from only 2.8% of fishing effort being in upper Lemmens Inlet. Only two male, and no female, recoveries were from outside the main study area despite a large number of traps fished 'elsewhere' by local fishermen (Fig. 4.8.1b, page 69), suggesting little movement of crabs from the study area. Similarly, male and female movement near Indian Island is restricted, as previously surmised, with 35 of 41 males, and 20 of 21 females, recovered near where they were tagged.

Histograms of mean distances moved also indicate limited movement (Fig. 4.11.4). Males and females moved (net distance), on average, less than 30 and 20 m per day, respectively. A simple two-dimensional random dispersion model estimated that the histogram of mean distances moved by males (Fig. 4.11.4) could be explained by a population whose gross movement rates (in  $\text{m} \cdot \text{d}^{-1}$ ) are described by the following log-normal distribution.



$$G = 280 \cdot \exp(1.1 \cdot v) \quad (4.11.1)$$

where:  $G$  is a point on the distribution of daily movement rates ( $m \cdot d^{-1}$ )  
 $v$  is a random normal deviate with a mean of 0 and a standard deviation of 1

Approximately 22% of males whose movement is described by the above distribution of movement rates would travel more than 10 km from their point of release after one year in an unbounded environment, assuming no mortality. Because of geographical and habitat boundaries, and high mortality, the percent leaving the study area is likely much lower.

Table 4.11.1. Abundance of female C. magister >145 mm CW in commercial traps in May and June of 1985 and 1986.

<u>Area Sampled</u>	<u>Female abundance</u> ( $n \cdot 100 \cdot \text{trap}^{-1} \cdot \text{soak day}^{-1}$ )	
	<u>1985</u>	<u>1986</u>
Upper Lemmens Inlet (A; Fig. 2.1)	7	13
Lemmens Inlet (B-D; Fig. 2.1)	15	8
Browning Passage (G; Fig. 2.1)	22	4
Near Indian Island (H; Fig. 2.1)	10	36
Main channel (F; Fig. 2.1)	429	138

Table 4.11.2. Densities of two to three year old ( $\approx 75$ -145 mm CW) C. magister from beam trawl samples near Indian Island.

<u>Date</u>	<u>Density (<math>n \cdot \text{ha}^{-1}</math>)</u>	
	<u>Male</u>	<u>Female</u>
20 Jun 1985	155	117
17 Oct 1985	96	172
8 May 1986	70	99

Table 4.11.3. Summary of tag recoveries, by location, of sublegal- and legal-sized male *C. magister* between April 1985 and August 1986. The number of trap hauls was determined by interviewing fishermen. Only records from fishermen whose effort was known are reported. Except where noted, recoveries were from within the study area as defined in Fig. 2.1 (page 9).

Location where crabs were <u>tagged</u>	Trap hauls <u>n</u> <u>(%)</u>	Number <u>Tagged</u>	Number of recoveries <sup>a</sup> ( <u>Mean days-at-large</u> )						
			<u>Where</u> <u>tagged</u>	<u>Up</u> <u>Inlet</u>	<u>Down</u> <u>Inlet</u>	<u>Toward</u> <u>Open</u> <u>Ocean</u>	<u>Toward</u> <u>Browning</u> <u>Passage</u>	<u>Toward</u> <u>Indian</u> <u>Island</u>	<u>Total</u>
Upper Lemmens Inlet (A; Fig. 2.1)	2234 (2.8)	1686	116 (93)	-	189 (157)	1 <sup>c</sup> (545)	-	-	306
Middle Lemmens Inlet (B; Fig. 2.1)	8655 (11.0)	1653	132 (116)	68 (132)	263 (170)	-	-	-	463
Lower Lemmens Inlet (C,D; Fig. 2.1)	16165 (20.5)	595	86 (118)	17 (143)	-	34 <sup>d</sup> (156)	7 (102)	-	144
Browning Passage (G; Fig. 2.1)	1053 (1.3)	85	7 (173)	14 (125)	-	4 (219)	-	0	25
Near Indian Island (H; Fig. 2.1)	9606 (12.2)	166	35 (154)	-	-	-	6 (124)	-	41
Rest of study area (Fig. 2.1)	25294 (32.1)	215	63 (151)	2 (166)	-	-	2 (135)	-	67
Elsewhere <sup>b</sup>	15729 (20.0)	0	-	-	-	-	-	-	-
Total	78736	4400	-	-	-	-	-	-	1046

<sup>a</sup> These areas are expressed relative to the area where the crabs were tagged. A dash (-) indicates an invalid category for assessing tag recoveries in this manner, not zero (0) recoveries.

<sup>b</sup> Outside the study area but still in SA 24.

<sup>c</sup> Recovered outside the study area.

<sup>d</sup> One male recovered outside the study area after 370 days at large.

Table 4.11.4. Summary of tag recoveries, by location, of female *C. magister* between April 1985 and August 1986. The number of trap hauls was determined by interviewing fishermen. Only records from fishermen whose effort was known are reported. All recoveries were from within the study area as defined in Fig. 2.1 (page 9).

Location where crabs were tagged	Trap hauls n	Number (%) Tagged	Number of recoveries <sup>a</sup> (Mean days-at-large)						Total
			Where tagged	Up Inlet	Down Inlet	Toward Open Ocean	Toward Browning Passage	Toward Indian Island	
Upper Lemmens Inlet (A; Fig. 2.1)	2234	(2.8)	495	6 (125)	-	11 (112)	-	-	17
Middle Lemmens Inlet (B; Fig. 2.1)	8655	(11.0)	540	13 (97)	4 (56)	14 (179)	-	-	31
Lower Lemmens Inlet (C,D; Fig. 2.1)	16165	(20.5)	334	6 (96)	2 (91)	-	4 (197)	0	12
Browning Passage (G; Fig. 2.1)	1053	(1.3)	12	0	1 (68)	-	0	0	1
Near Indian Island (H; Fig. 2.1)	9606	(12.2)	147	20 (283)	-	-	1 (518)	-	21
Rest of study area (Fig. 2.1)	25294	(32.1)	635	41 (230)	1 (40)	-	1 (57)	-	43
Elsewhere <sup>b</sup>	15729	(20.0)	0	-	-	-	-	-	-
Total	78736		2163	-	-	-	-	-	125

<sup>a</sup> These areas are expressed relative to the area where the crabs were tagged. A dash (-) indicates an invalid category for assessing tag recoveries in this manner, not zero (0) recoveries.

<sup>b</sup> Outside the study area but still in SA 24.

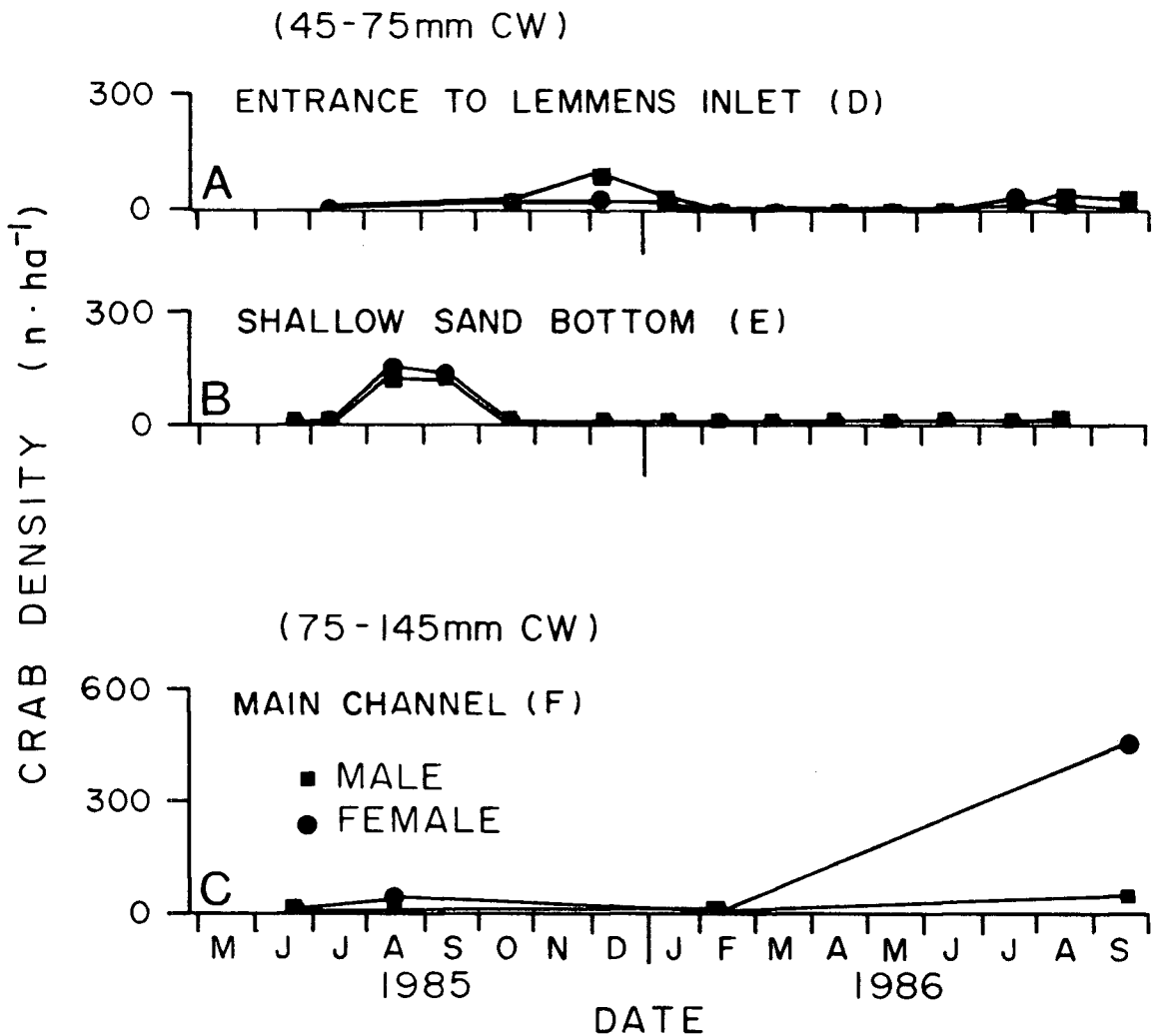


Figure 4.11.1. Time series of densities for one year old ( $\approx 40-75$  mm CW) male and female *C. magister* in the entrance to Lemmens Inlet (A), and on the shallow sand bottom of an exposed shore (B). Time series of densities of two to three year old ( $\approx 75-145$  mm CW) male and female *C. magister* in the main channel out to sea (C). The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).

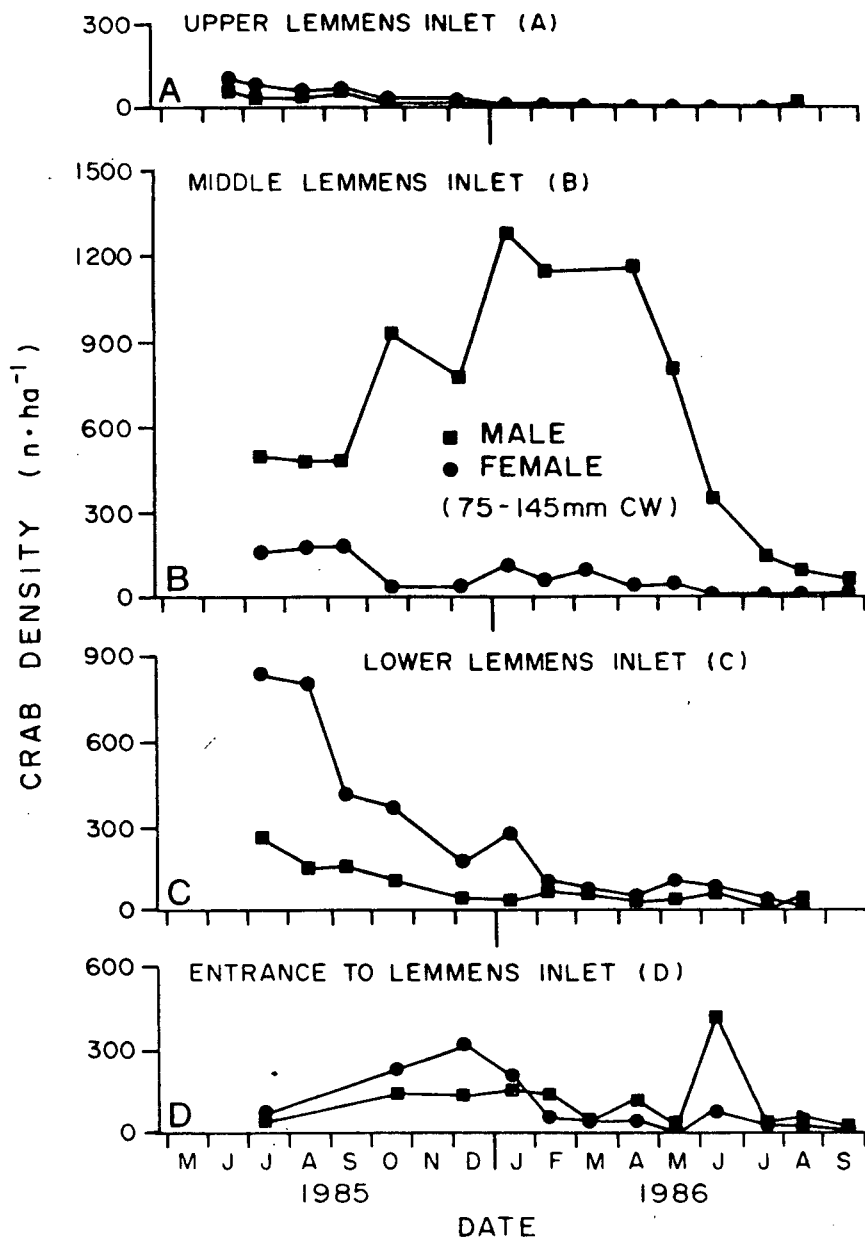


Figure 4.11.2. Time series of densities for two to three year old ( $\approx 75-145$  mm CW) male and female *C. magister* in Lemmens Inlet. The capital letters in parentheses identify these areas in Fig. 2.1 (page 9).

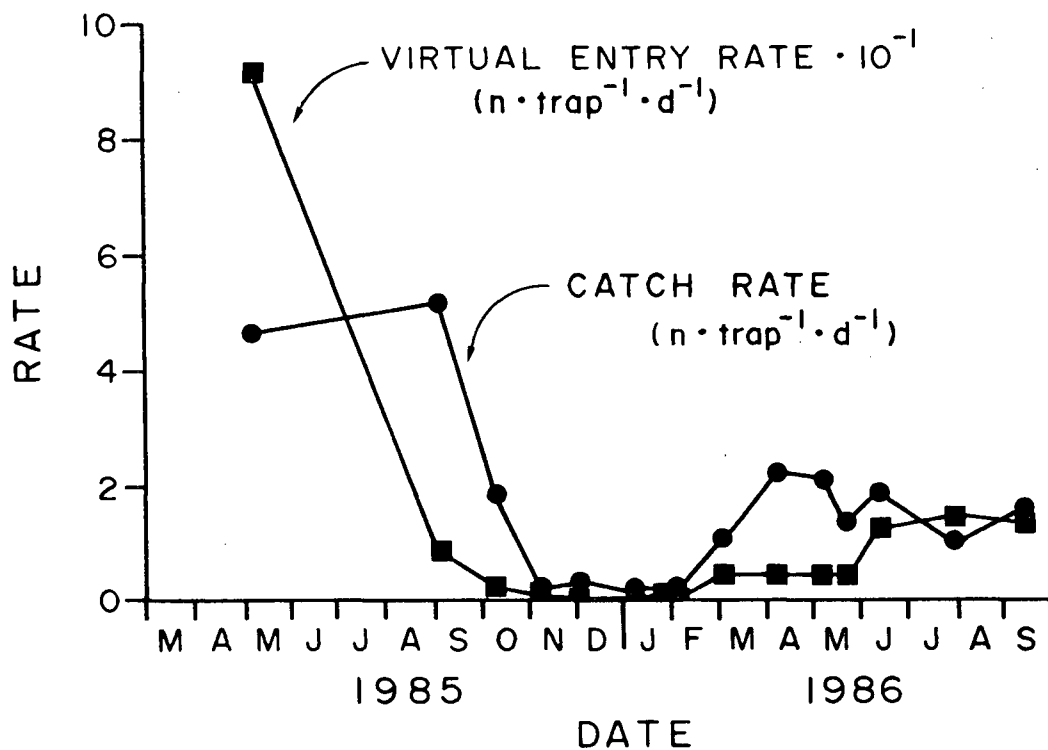


Figure 4.11.3. Time series comparison of two indices of abundance for female *C. magister* (>145 mm CW) in the study area, but excluding Lemmens Inlet, Browning Passage, and near Indian Island, where female densities were generally low (Table 4.11.1). 'Virtual entry rates' were estimated as in Section 4.9.

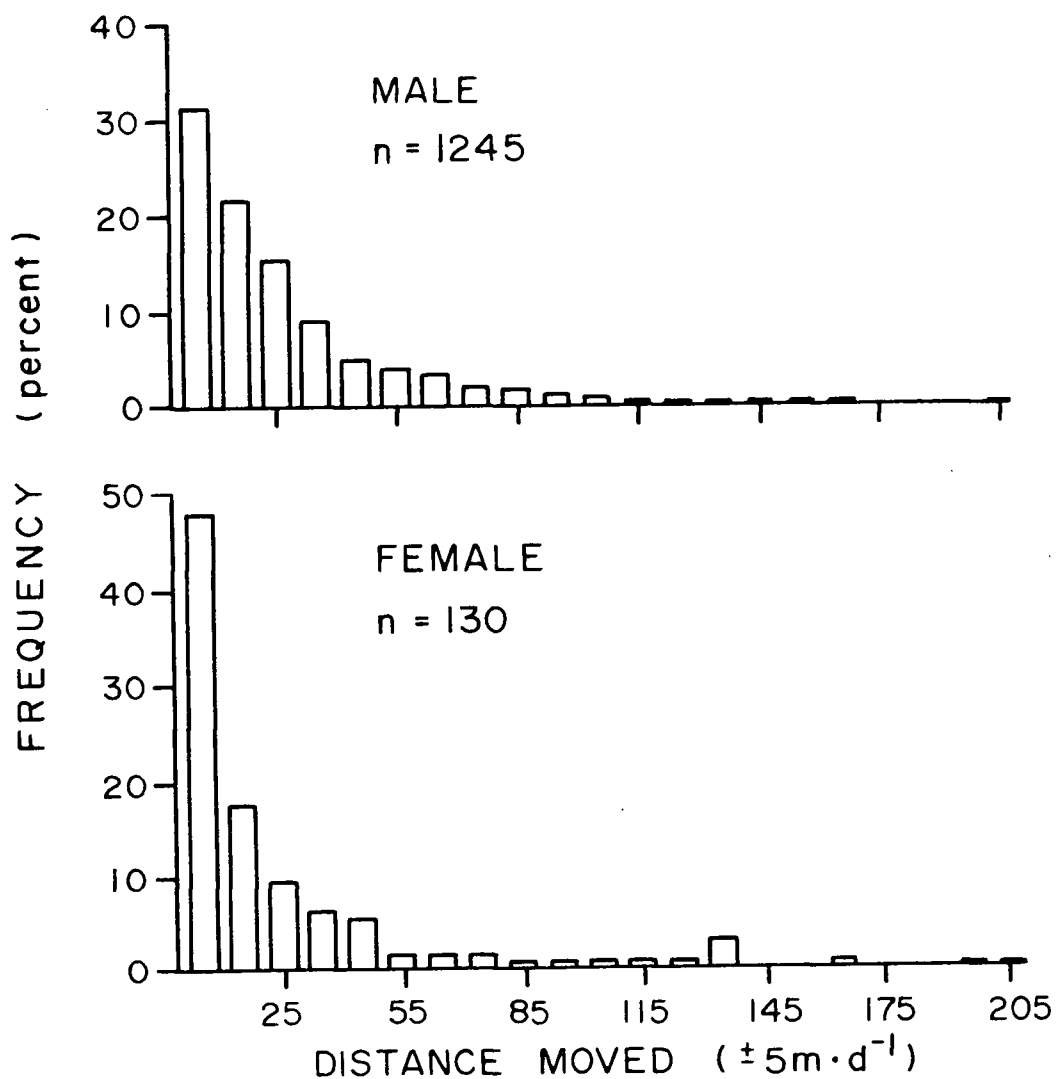


Figure 4.11.4. Frequency distributions of mean daily movement rates for male and female *C. magister*. Crabs were recovered after a mean of  $\approx 150$  days-at-large.

#### 4.12 TAG RETENTION AND TAG INDUCED MORTALITY

Tag retention was estimated from recoveries of 850 double tagged sublegal-sized males released in spring 1986. Tag retention was analyzed separately for males that moulted, and those that did not moult, before being recovered.

The number of males recovered that did not moult and retained both or one tag was 59 and 4, respectively, for a retention rate of 96.8%. The mean and median times-at-large for these males were 83 and 69 days, respectively.

Number of double tagged crabs recovered:	63
Expected number of tags:	$63 \cdot 2 = 126$
Observed number of tags:	$(59 \cdot 2) + 4 = 122$
Percent retention:	$(122 \div 126) \cdot 100 = 96.8$

The number of males recovered that retained both or one tag through a moult was 64 and 1, respectively, for a retention rate of 99.2%.

Number of double tagged crabs recovered:	65
Expected number of tags:	$65 \cdot 2 = 130$
Observed number of tags:	$(64 \cdot 2) + 1 = 129$
Percent retention:	$(129 \div 130) \cdot 100 = 99.2$

Because the tag retention rate is apparently high, tag loss was assumed to be negligible in mortality estimates (Section 4.13).

Informal observations of tagged and untagged C. magister held in tanks at the Pacific Biological Station for several months did not indicate a higher mortality rate due to a crab having been tagged.



#### 4.13 FISHING AND NATURAL MORTALITY OF MALES

The mark-recovery program provided estimates of fishing and natural mortality for male C. magister. (No estimates were made of female natural mortality because an insufficient number was tagged and recovered). The logarithms of the number of recoveries of males tagged, released and recovered when sublegal size (145-155 mm CW) are plotted for consecutive one month intervals in Fig. 4.13.1. These results were obtained from the four fishermen and myself, who recorded all occurrences of sublegal-sized males in their traps, then released them. The effort of all four fishermen was consistent over the study period.

The annual instantaneous rate of disappearance of these males is the negative slope of the linear relationship (SAS Institute Inc. 1985) in Fig. 4.13.1 (Table 4.13.1) times 365 days ( $=3.48$ , 95% C.I. is 2.90-4.06) (Gulland 1983). Since movement from the study area (Section 4.11), tag loss and tag induced mortality (Section 4.12) seem to be small contributors to the disappearance of tagged crabs, this rate mainly measures the combination of  $M$  (the annual instantaneous rate of natural mortality) and the instantaneous rate of moulting into legal size. The slope of Fig. 4.13.1 can be considered a maximum estimate of  $M$  while these males remain in this same instar. A quadratic curve applied to the data in Fig. 4.13.1 (Table 4.13.2) suggests that the rate of disappearance of these males increases as the time within an instar increases.

Table 4.13.1. Statistics of the linear relationship in Fig. 4.13.1 from which the annual instantaneous rate of disappearance of sublegal-sized (145-155 mm CW) male C. magister was estimated. The relationship has the form  $Y = a + b \cdot X$ ; where Y is the logarithm of the number of recoveries within consecutive one month intervals, and X is the time-at-large in days.

<u>Parameter</u>	<u>Estimate</u>	<u>Standard error</u>
a	5.99	0.25
b	-9.54E-3	0.81E-3

Table 4.13.2. Statistics of the quadratic relationship in Fig. 4.13.1 which suggests the mortality rate may increase as the time-at-large for sublegal-sized (145-155 mm CW) male C. magister increases. The relationship has the form  $Y = a + b \cdot X + c \cdot X^2$ ; where Y is the logarithm of the number of recoveries within consecutive one month intervals, and X is the time-at-large in days.

<u>Parameter</u>	<u>Estimate</u>	<u>Standard error</u>
a	4.92	0.40
b	3.65E-5 <sup>a</sup>	316.0E-5
c	-1.67E-5	0.54E-5

<sup>a</sup> Not significantly different from b=0.0.

Figure 4.13.2 plots the recovery of 182 males, legal size when tagged and released (n=341), for consecutive 15 day intervals, for a total recovery of 53.4% from all fishermen. The total annual instantaneous rate of disappearance of legal-sized males (Z) is the negative slope of the linear relationship in Fig. 4.13.2 (Table 4.13.3) times 365 days (=9.23, 95% C.I. is 7.23-11.23) (Gulland 1983, p. 110, Eqn. 4.33). A provisional and minimum estimate of the annual instantaneous rate of fishing

mortality (F) is 4.95 (=9.23·0.534). Therefore, an annual instantaneous rate of 4.29 accounts for the lack of recoveries for all other reasons. Again, since there is no significant movement of tagged crabs from the study area over this time, or tag loss or tag induced mortality, these tags were probably not recovered because of (1) natural mortality, and (2) they were missed by, or I did not obtain the tags from the fishermen.

---

Table 4.13.3. Statistics of the linear relationship in Fig. 4.13.2 from which the annual instantaneous rate of disappearance (Z) of legal-sized male C. magister was estimated. The relationship has the form  $Y = a + b \cdot X$ ; where Y is the logarithm of the number of recoveries within consecutive 15 day intervals, and X is the time-at-large in days.

---

<u>Parameter</u>	<u>Estimate</u>	<u>Standard error</u>
a	4.23	0.27
b	-2.53E-2	0.28E-2

---

From recoveries of males, 125-155 mm CW when tagged, and legal size when recovered, a seasonal profile of moulting into legal size was obtained (Fig. 4.13.3). From the revised estimate of F (5.11-6.90) below, the time to a 50% expectation of recovery for a legal-sized male is 37-50 days. Since Fig. 4.13.3b covers a time period much greater than this, it closely resembles the seasonality of moulting of sublegal-sized males 125-155 mm CW into legal size. Moulting occurs all year, but mostly in summer.

Figure 4.13.3 shows that survivorship to the next instar decreases with size, with a smaller percent of crabs 140-155 mm

CW attaining legal size than those 125-140 mm CW. This seems not to be a result of insufficient intermoult time for the larger crabs. Most tagged crabs were monitored for 400-600 days, and nearly all moulting was observed after less than 400 days at large (Fig. 4.13.4, Table 4.13.4). The annual instantaneous rate of disappearance for males 145-155 mm CW of 3.48 (Fig. 4.13.1, Table 4.13.1) also suggests this since <3% of these crabs were present at this size after 400 days at large. Figure 4.13.4 shows a trend toward a longer intermoult period with increasing size. The length of the intermoult period cannot be precisely determined from this relationship because it is not known how long after moulting crabs were tagged, therefore Fig. 4.13.4 provides only a minimum estimate of the length of the intermoult period.

---

Table 4.13.4. Statistics of the linear relationship in Fig. 4.13.4 estimating the mean time-at-large for recovered tagged sublegal-sized male C. magister. The relationship has the form  $Y = a + b \cdot X$ ; where Y is the time to recovery (in days), and X is the pre-moult carapace width.

---

<u>Parameter</u>	<u>Estimate</u>	<u>Standard error</u>
a	-628.4	113.0
b	6.22	0.81

---

The percent of sublegal-sized males expected to survive to legal size is estimated from the number of recovered tagged legal-sized males that were tagged when sublegal size (Table 4.13.5). Calculation of mortality from these data is somewhat

hindered by an uncertain estimate of the proportion of tagged legal-sized males caught that I observed. I will refer to this proportion as compliance. Since 0.534 of the 341 legal-sized males tagged and released were recovered (Fig. 4.13.2), this represents a minimum estimate of compliance. This estimate can be revised as explained below.

From categories 145-150 and 150-155 mm CW from Table 4.13.5, which are composed of males close to legal size within the 155.0 mm instar, M can be provisionally estimated at 4.48 (i.e. the negative log of the proportion recovered, adjusted for the time-at-large).

$$M = -\ln(53 \div 2246) \cdot (365 \div 305) \quad (4.13.1)$$

A revised estimate of M, incorporating an adjustment for compliance (C), is:

$$M = 4.48 + \ln(C) \quad (4.13.2)$$

From Fig. 4.13.2 and Table 4.13.3, which document the recovery of males tagged, released and recovered when legal size, and in the 155.0 mm instar:

$$Z = 9.23 \pm 1.02 \quad (4.13.3)$$

$$F = (0.534 \div C) \cdot Z \quad (4.13.4)$$

$$M = Z - F \quad (4.13.5)$$

therefore,

$$M = Z - (0.534 \div C) \cdot Z \quad (4.13.6)$$

If one assumes that  $M$  and  $C$  are the same for both analyses, an estimate of  $C$  can be obtained by solving Eqns. 4.13.2 and 6 simultaneously for a single estimate of  $M$ . Within the 95% confidence limits of  $Z$  (7.23-11.23), for  $Z < 9.59$  no corresponding estimate of  $M$  is obtainable because  $C$  must, but obviously cannot, exceed 1.0. For  $Z=11.23$ ,  $C$  is estimated at 0.869, and  $M$  at 4.33. The range of  $M$  for  $C$  ranging from 0.869-1.00 is 4.33-4.48. The equivalent range for  $F$  is 5.11-6.90. In consideration of the close monitoring of this fishery, I accept the lower compliance estimate of 0.869 as plausible. Table 4.13.5 reports estimates of  $M$  for 5 mm CW intervals from 125-155 mm assuming the more conservative estimate of compliance of 0.869. As was apparent in Fig. 4.13.3, the results suggest size-dependent mortality, larger crabs having the lower survivorship.

The estimate of  $M=4.33-4.48$  for crabs 145-155 mm CW is higher than the maximum estimate of  $M=3.48$ , for essentially the same size range, obtained from Fig. 4.13.1. Since the latter estimate applies only to males still sublegal size, the best explanation for this discrepancy is a higher mortality rate for males during, or while soft-shelled following, the moult to legal size. If this is the correct explanation then the above assumption that the estimates of  $M$  should be similar for the analyses based on the data in Tables 4.13.3 and 5 is not strictly true. Thus, fishing mortality ( $F$ ) may be underestimated and  $M$  may be overestimated.

No experiments were attempted to distinguish between (1) the disappearance of sublegal-sized males due to moulting to legal size and disappearance due to mortality in Fig. 4.13.1, and (2) between pre- and immediately post-moult mortality in Table 4.13.5, so the discrepancies in the estimates of M cannot be further resolved. However, one can conclude that the more the disappearance of sublegal males in Fig. 4.13.1 is attributable to moulting, the greater the moult, or post-moult, mortality.

Size frequency analysis on trap sampled males for each fishery, including the lightly fished Holberg Inlet fishery, could not detect an 183.8 mm instar. This is consistent with the mark-recovery results presented in this section which indicate low survivorship from the 155.0 mm to the 183.8 mm instar.

---

Table 4.13.5. Summary of survivorship to legal size of male *C. magister* which were tagged when sublegal size, and recovered when legal size, for 5 mm intervals from 125-155 mm CW.

---

Pre-moult carapace width (mm)	Number tagged	Recoveries n (%)		Percent surviving to legal size <sup>a</sup>	Mean days at large <sup>b</sup>	Instantaneous annual mortality
125-130	168	20	11.9	32.1	165	2.87
130-135	310	50	16.1	24.0	196	2.96
135-140	366	52	14.2	19.2	227	2.91
140-145	499	35	7.0	9.5	258	3.56
145-150	1027	28	2.7	3.7	289	4.37
150-155	1219	25	2.1	2.8	320	4.27

---

<sup>a</sup> Calculated by multiplying the percent recovered in each 5 mm CW interval by 1.15 to compensate for the more conservative estimate of only 86.9% of tagged legal-sized crabs landed being observed. The percent recovered in intervals 125-130 and 130-135 mm CW was further multiplied by 2.0 and 1.1, respectively, because only 50% and 90% of crabs this size are expected to attain legal size with their next moult.

<sup>b</sup> From regression parameters of Fig. 4.13.4 ( $Y = -628.4 + 6.22 \cdot X$ ).

---

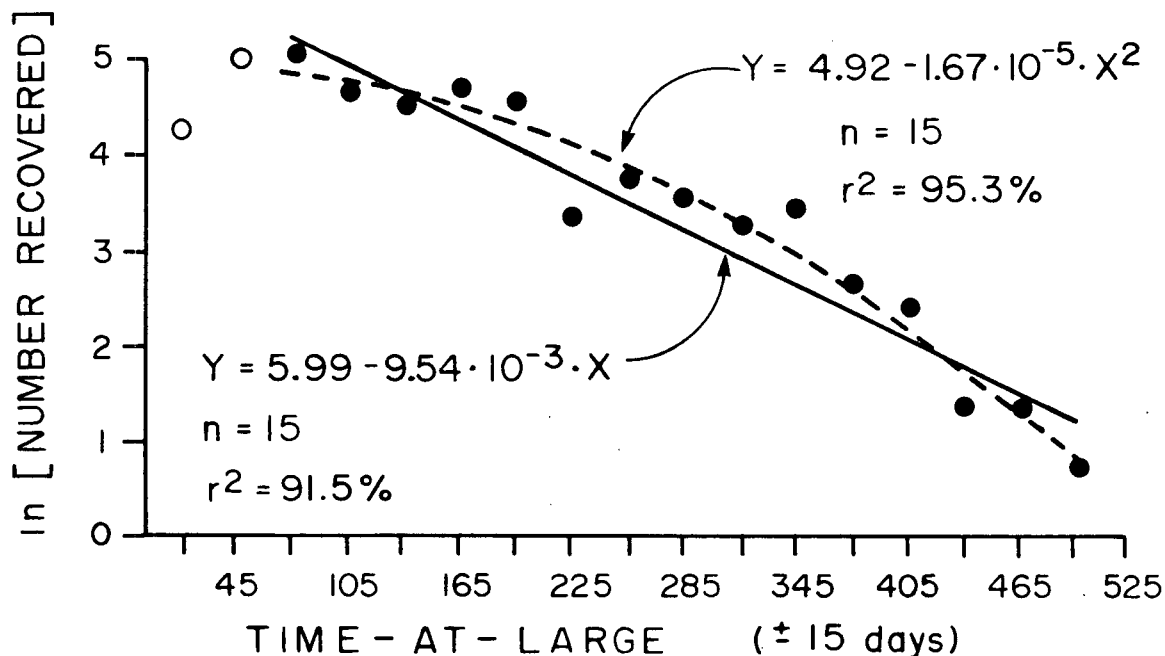
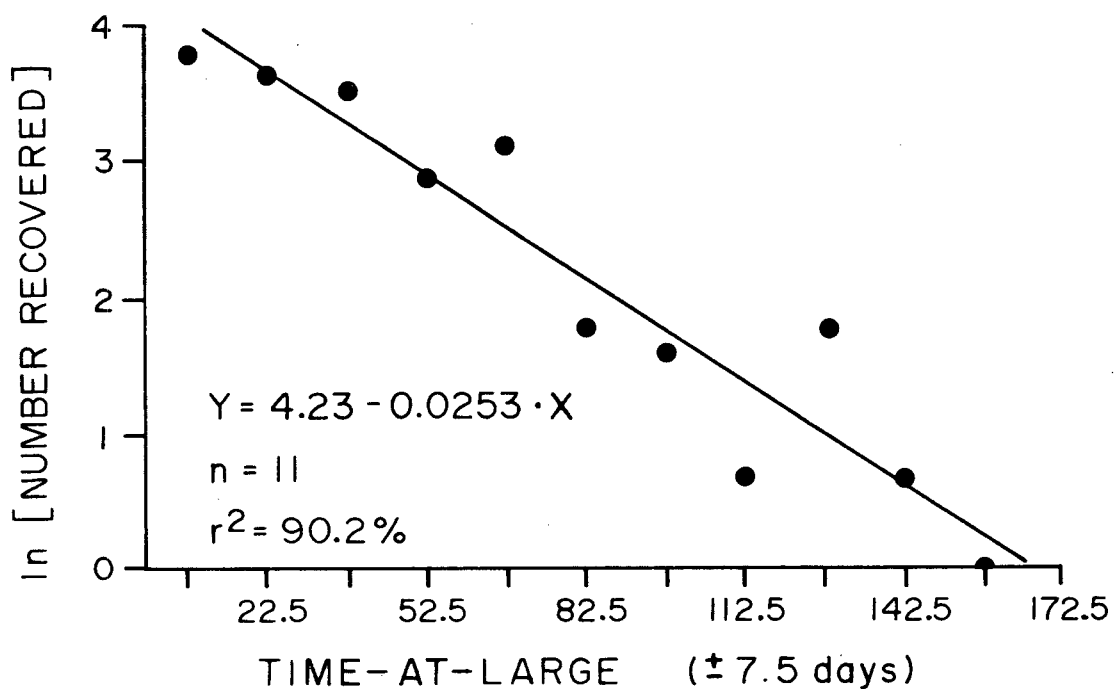


Figure 4.13.1. Linear and quadratic regressions of recoveries over time for tagged male *C. magister* released and recovered as sublegal-sized crabs 145-155 mm CW. Most tagging was done from May-July 1985. The open circles were not included in the regression analyses because fishermen were not well prepared for the mark-recovery program at this time.





---

Figure 4.13.2. Linear regression of recoveries over time for 341 tagged male C. magister released and recovered as legal-sized crabs, mostly in spring 1986.

---

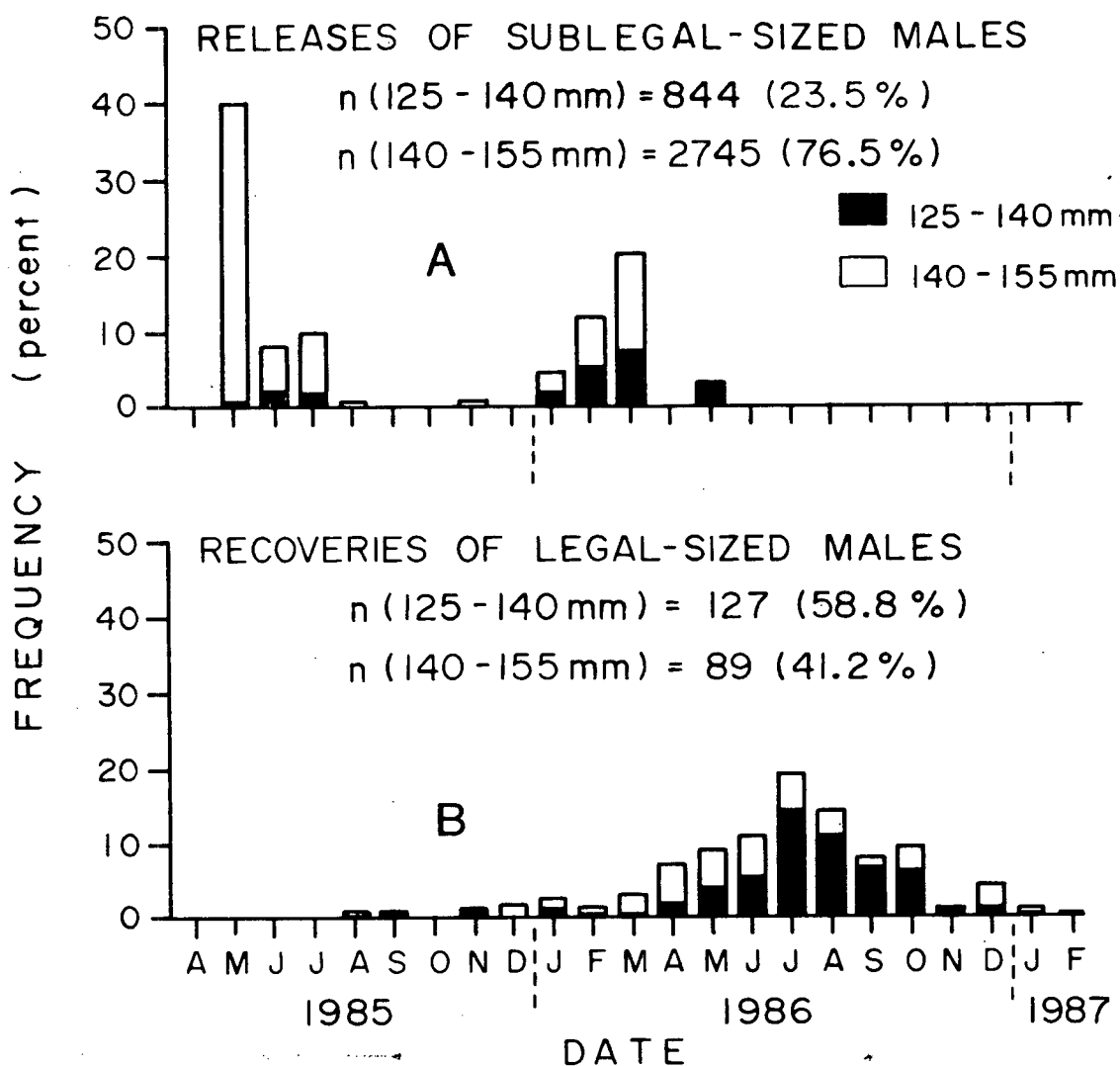
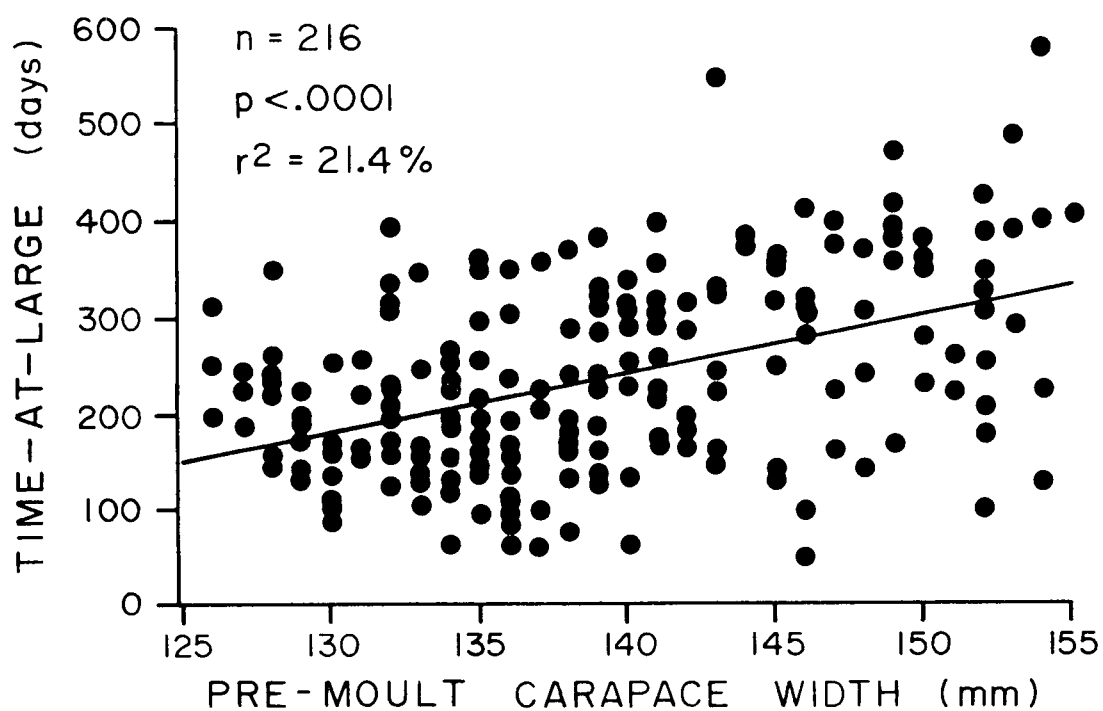


Figure 4.13.3. (A) Frequency distribution of release dates of sublegal-sized male *C. magister*. (B) Frequency distribution of recovery dates for those crabs released in (A) and recovered as legal-sized crabs.



---

Figure 4.13.4. Linear regression of time-at-large for male C. magister, tagged and released when sublegal size and recovered when legal size, on pre-moult carapace width.

---

#### 4.14 FISHING INTENSITY AND FEMALE CATCH CURVES IN SELECTED FISHERIES

Table 4.14.1 compares fishing intensity in four regional fisheries as defined by Statistical Area. These statistical areas do not differ markedly in area. The quantity of males landed, the number of days fished, the number of vessels fishing, and the number of sales in these regional fisheries are relative indicators of fishing effort. The degree of exploitation and the virtual entry rate of legal-sized males are indicators of fishing impact. These impacts were determined as in Section 4.9. The Fraser delta fishery appears heavily exploited, while the Holberg Inlet fishery is lightly exploited. Two other fisheries, near Tofino and in Dixon Entrance experience intermediate fishing intensity, except that this study shows that since 1985 the C. magister population near Tofino has experienced heavy fishing.

Despite females not being fished, the catch curves (Ricker 1975) for females caught by these fisheries (Fig. 4.14.1) suggest a lower survivorship to larger instars in the more heavily fished populations. The catch curve for each fishery combines commercial samples from the two consecutive years when each of these fisheries were sampled. Combining samples from consecutive years was suggested by Ricker (1975) to reduce the influence of a possibly dominant age-class. Prior to plotting the catch curves the samples were standardized to obtain virtual entry rates as in Section 4.9. Survivorship of females to larger instars in the

heavily fished Fraser delta fishery is much lower than that for the lightly fished Holberg Inlet fishery, while the catch curves for the other two regions are intermediate.

It is unlikely that the absence of large females in the intensely exploited Fraser delta fishery results from legal-sized females having been harvested because the size frequency distributions do not show a discontinuous decrease in abundance at legal size. It also seems unlikely this pattern results from increased mortality due to trapping and excessive handling in an intensive fishery. Mortally injured or dead crabs were seldom seen in traps or trawls during this study. When such crabs were encountered they were well represented by connected body parts, including the carapace, suggesting little unseen mortality occurs within traps. If mortality in traps is low, despite the artificially high density of crabs in traps, then trapping and handling induced mortality outside traps would be expected to be lower. Thus, there is no direct evidence to suggest that lower survivorship of females in intense male-only fisheries is due to trapping and handling.

Since females moult and mate in the company of a larger male, many of whom may have been removed in a heavily fished population, it is conceivable that females may not achieve larger instars in heavily fished populations because of a lack of legal-sized males for mating partners. The following section elaborates on this possibility, and its potential consequences for population egg production.

Table 4.14.1. Comparisons among different measures of fishing effort, and fishing impact, on male *C. magister* populations in four regional fisheries defined by Statistical Area (SA). The statistical areas do not differ markedly in area. Annual fishing statistics include the metric tonnes landed (t) and the number of days fishing (DF).

Region	Degree of exploitation <sup>a</sup>	Virtual entry rate <sup>b</sup>	Number of vessels <sup>c</sup>	Number of sales <sup>c</sup>	Annual fishing statistics					
					1983		1984		1985	
					t	DF	t	DF	t	DF
Holberg Inlet (SA 27)	17 <sup>d</sup>	641	10	37	3	73	5	116	5	185
Dixon Entrance (SA 1)	45 <sup>e</sup>	84	25	135	136	394	146	457	160	474
Near Tofino (SA 24)	≈75 <sup>f</sup>	103	27	434	136	1869	110	1228	152	1391
Fraser delta (SA 29)	86 <sup>g</sup>	49	119	1307	274	2341	341	3636	353	3662
British Columbia Total	-	-	-	-	959	12987	1155	15731	1165	16851

<sup>a</sup> The percent of the legal-sized males in the 155.0 mm instar taken by the fishery near the end of the season. See Section 4.9 for an explanation of this estimate.

<sup>b</sup> The number of legal-sized male crabs that would enter 100 traps if the entry rate was not reduced (1) by crabs within traps inhibiting the entry of more crabs, and (2) changes in bait effectiveness. See Section 4.7 for a more complete explanation.

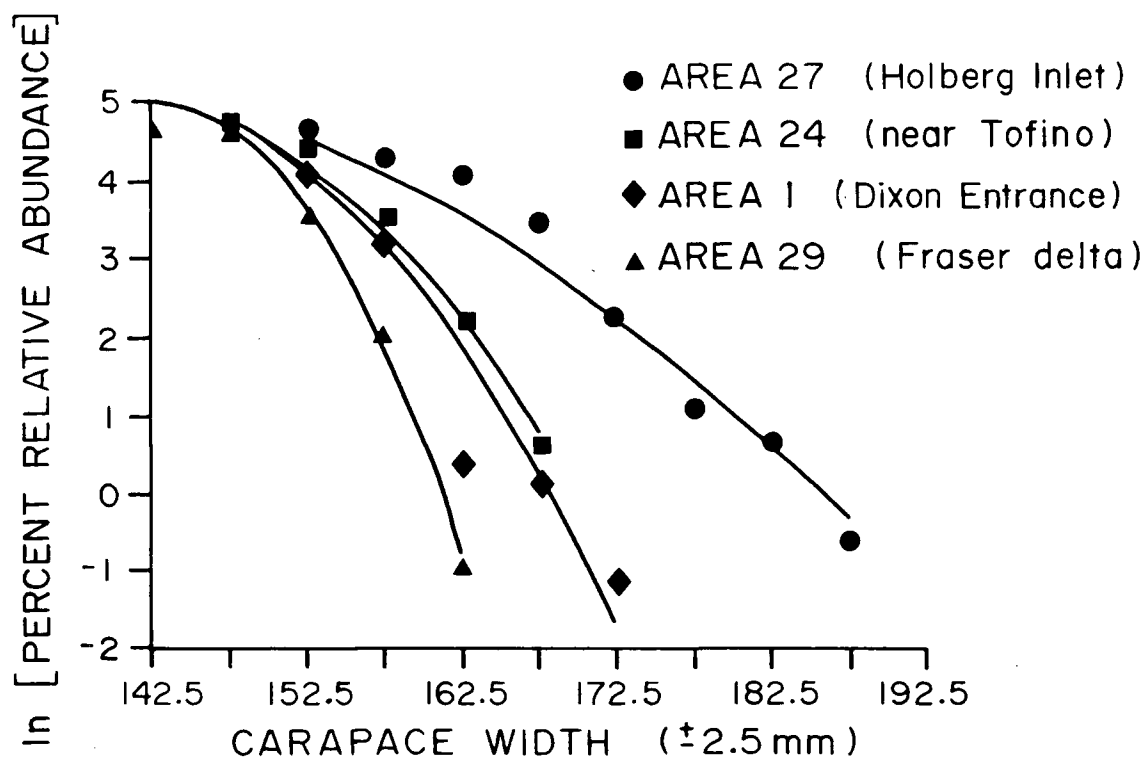
<sup>c</sup> In 1984.

<sup>d</sup> In December 1984.

<sup>e</sup> Mean of October 1983 and 1984.

<sup>f</sup> From Figure 4.9.2.

<sup>g</sup> Mean of October 1984 and 1985.




---

Figure 4.14.1. Comparison of catch curves (Ricker 1975) for females from four regional C. magister fisheries defined by Statistical Area in British Columbia.

---

## 5 YIELD- AND EGGS-PER-RECRUIT MODEL

### 5.1 DEVELOPMENT

This section evaluates trade-offs in C. magister yield- and eggs-per-recruit resulting from altering the minimum legal size limit for males. Model structure and estimates for critical population variables (e.g. growth and mortality) are based on information obtained in this study supplemented by information on female growth, mortality and fecundity from Hankin et al. (1985).

Relative yield-per-recruit was determined by accounting the predicted catch of males, by weight, for different minimum legal size limits. Dry weight was determined from carapace width using Eqn. 4.7.3.4 (page 55). As recommended by Caddy (1986), the yield-per-recruit analysis is based on moult increments-at-size, moult frequency and moult probabilities, acknowledging discontinuous growth. Some workers have used a von Bertalanffy growth model for crustaceans when instars were not easily distinguished and a continuous growth model seemed an appropriate simplification. With C. magister having few moults and large moult increments-at-size for the sizes relevant to this analysis, this would not have been appropriate. The determination of yield- and eggs-per-recruit is explained in the following paragraphs.

The model includes the 102.9, 128.0, 155.0 and 183.8 mm male, and the 100.7, 119.4, 135.5, 149.4 and 161.4 mm female, instars defined by the size frequency analyses in Section 4.6.



The smallest male and female instars are dominant in summer two years after settlement. Moulting timing, and the time when particular instars dominate (Table 5.1.1), are estimated from Tables 4.6.3 and 4 (pages 41 and 42), and Fig. 4.13.3 (page 105). All individuals in male and female instars for each age-class are accounted. For females an additional four vectors account individuals in each age-class which failed to moult for 1-4 years. Male and female growth was modeled by creating a normal size distribution of 1 mm CW intervals for the smallest instars in Table 5.1.1, then incrementing this distribution by applying Eqns. 4.5.1 and 2 (moult increments-at-size, page 33) for males and females, respectively.

---

Table 5.1.1. The mean and standard deviation (mm) of normally distributed male and female C. magister instars for the age and time of year when they are nearly fully formed. Males become sexually active in the 155.0 mm instar.

---

	<u>Date</u>	<u>Male instars</u>	<u>Female instars</u>	
Age 2	Winter			
	Spring			
	Summer	102.9± 9.8	100.7±12.8	
	Autumn		119.4±11.0	egg producing
Age 3	Winter			females
	Spring	128.0±10.5		from
	Summer			this
	Autumn	155.0±11.2	135.5± 9.5	instar
Age 4	Winter			on
	Spring			
	Summer			assumes females in
	Autumn	183.8±12.0	149.4± 8.2	135.5 to 161.4 mm
Age 5	Winter	"		instars normally
	Spring	"		moult annually
	Summer	"		
	Autumn	"	161.4± 7.1	assumes males
				this size
				do not
				moult annually

---

Annual mortality rates are applied to the instars in Table 5.1.1 to determine the numbers-at-age for males and females. Annual instantaneous natural mortality (M) estimates for males were determined in this study. Female mortality estimates are from Hankin et al. (1985), who estimated M at 0.7-2.5, M increasing with increasing carapace widths for females >125 mm. A consideration of their mark-recovery methodology suggests M=0.7 is an underestimate because commercial traps do not effectively retain small crabs. As the smaller tagged crabs moult to larger sizes their occurrence in traps increases, thus misrepresenting relative abundance. Because of variability in the mortality estimates, I report yield- and eggs-per-recruit results for annual mortality estimates of 1.0, 2.5 and 4.0. Mortality rates are assumed constant for all sizes and ages. Considering the high mortality estimates, cohorts are followed to virtual extinction.

As suggested by the size frequency distribution of the occurrence of mating marks (Fig. 4.10.1, page 81), males are not considered sexually mature until they attain the 155.0 mm instar. Butler (1960) suggests males are mature at 100-110 mm CW, but mating marks on males this size were rare. Males this size would have difficulty finding mature females of a size that they could embrace since Fig. 4.4.1 (page 31) suggests males must mate with a female considerable smaller than themselves. Most males become

functionally mature after attaining 130 mm CW. This is consistent with their becoming functionally mature upon attaining the 155.0 mm instar.

Since one male can apparently mate with several females in one summer season (Butler 1960), an estimate of the maximum number of females mated by each male is required (F:M mating ratio). Such estimates elusive since natural behavior cannot be replicated in the laboratory, and observations of individual males in nature for a mating season are not possible. In a one week period I observed a male mate successfully with two females in a laboratory tank. Snow and Neilsen (1966) report that mating required 10 days for the pair they observed. Over a mating season the F:M mating ratio is potentially large.

In consideration of the uncertainty in such estimates, I report eggs-per-recruit results for maximum F:M mating ratios of 5, 10 and 20:1. Since there are no data to develop a functional response relationship between the F:M mating ratio and female density, I must assume that the maximum number of females that can be mated by a male is not modified by female density. It is reasonable to expect that at any female density males would attempt to maximize their evolutionary fitness by maximizing the number of females with which they mate.

For females the 100.7 mm instar is considered the first sexually mature instar. Further moults require a female to have a male partner. As reported in Fig. 4.3.1 (page 29), no sexually

mature females were found without sperm packs indicating that females do not attain larger sizes without having mated. P.W. Wild (cited in Hankin et al. 1985) and G.S. Jamieson (pers. comm.) have both observed females moulting in the absence of males, but this is not necessarily typical for females. The data of Hankin et al. (1985), and the female catch curves in Section 4.14, suggest this is not the case for females >145 mm CW.

Hankin et al. (1985) report that annual moulting probabilities for females in central California decline precipitously from near 1.0, for a female 130 mm CW, to near 0.0, for a female 145 mm CW. Females 140 mm CW and larger require a male at least 155 mm CW for a mating partner (Fig. 4.4.1, page 31), so a possible explanation for females not moulting to larger instars is a lack of legal-sized males. California fisheries remove a large portion of legal-sized males each year (Methot and Botsford 1982). The lower survivorship of females to larger instars in heavily exploited C. magister populations in British Columbia (Section 4.14) also suggests a lack of mating and moulting for larger females. Substantiating this is the conclusion that exploitation rates of legal-sized males can be high enough to markedly reduce their mating potential (Fig. 4.10.3, page 83).

The proportion of females in each 1 mm CW interval moulting each year was determined as follows. All males in the 120-121 mm CW interval within either the 155.0 or 183.8 mm instars were distributed proportionately among females available for mating

within the carapace width limits defined in Fig. 4.4.1 (page 31). This was repeated for all 1 mm CW intervals >121 mm CW. The results for each 1 mm CW interval were then multiplied by the F:M mating ratio to define the potential number of females mated for each interval. The proportion of females mated in each 1 mm CW interval is the potential number of females mated divided by the total number of females available, to a maximum of 1.0.

Hankin et al. (1985) show that winter egg production by females which did not mate and moult in the current season is lower than for females which did mate and moult. Their data are qualitative, and do not define a relationship between egg production and the number of years since a female mated and moulted. Therefore, this model evaluates egg production for extreme estimates of the annual rate of decrease in egg production by females which fail to undergo an annual moult. The rates evaluated were 1.0 (i.e. no decrease) and 0.0 times the egg production for the previous year.

Female fecundity (E) as a function of carapace width (CW, mm) was estimated using the following relationship from Hankin et al. (1985).

$$E = -593000 + 9670 \cdot CW \quad (5.1.1)$$

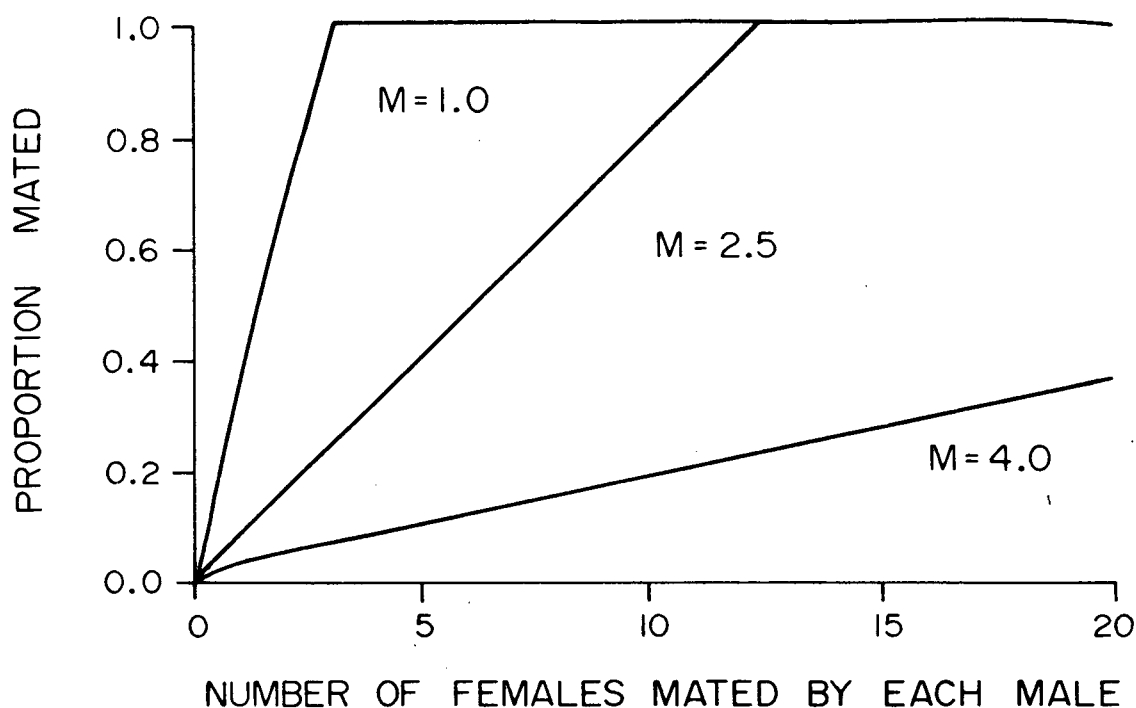
To be consistent with the minimum size of females observed with eggs in this study only females >100 mm CW within instars larger than the 100.7 mm instar produced eggs. This is

equivalent to a pre-moult carapace width of 78 mm (from Eqn. 4.5.2, page 33), close to the smallest size of female observed in a mating embrace.

## 5.2 RESULTS

Figure 5.2.1 indicates that a F:M mating ratio of  $\approx 10-15:1$  assures near maximum population egg production when  $M=2.5$ . These results also provide some insight for evaluating estimates of  $M$ . For example, for  $M=4.0$ , an extremely high F:M mating ratio ( $\approx 60:1$ ) would be required for males to mate all females. At such a high mortality rate, then considering the time involved in mating, a mean F:M mating ratio of 60:1 for the male population could not be achieved because of short life expectancies. This would seem to indicate that  $M=4.0$  is unlikely for mature C. magister, since no mature females were ever observed that had not been mated. Alternatively, for  $M=1.0$ , a F:M mating ratio as low as 3:1 is sufficient to ensure all females are mated. Since sublegal-sized males with extensive and deep scars on the chelipeds (mating marks) were common in this study and in Butler's (1960) study, one would surmise that many more than three females were mated by these males. Consequently, a maximum F:M mating ratio of  $\approx 10-15:1$  with  $M \approx 2.5$  seem the more plausible estimates for these processes.

If  $M=2.87-4.48$  (as estimated in Section 4.13 of this study) is an accurate annual estimate, then mortality rates must be lower during the time of year when males are reproductively




---

Figure 5.2.1. Relative egg production by C. magister populations as a function of the F:M mating ratio, and for three estimates of M. These results are not noticeably sensitive to the annual rate of decrease in egg production by females who fail to mate and moult in previous years.

---

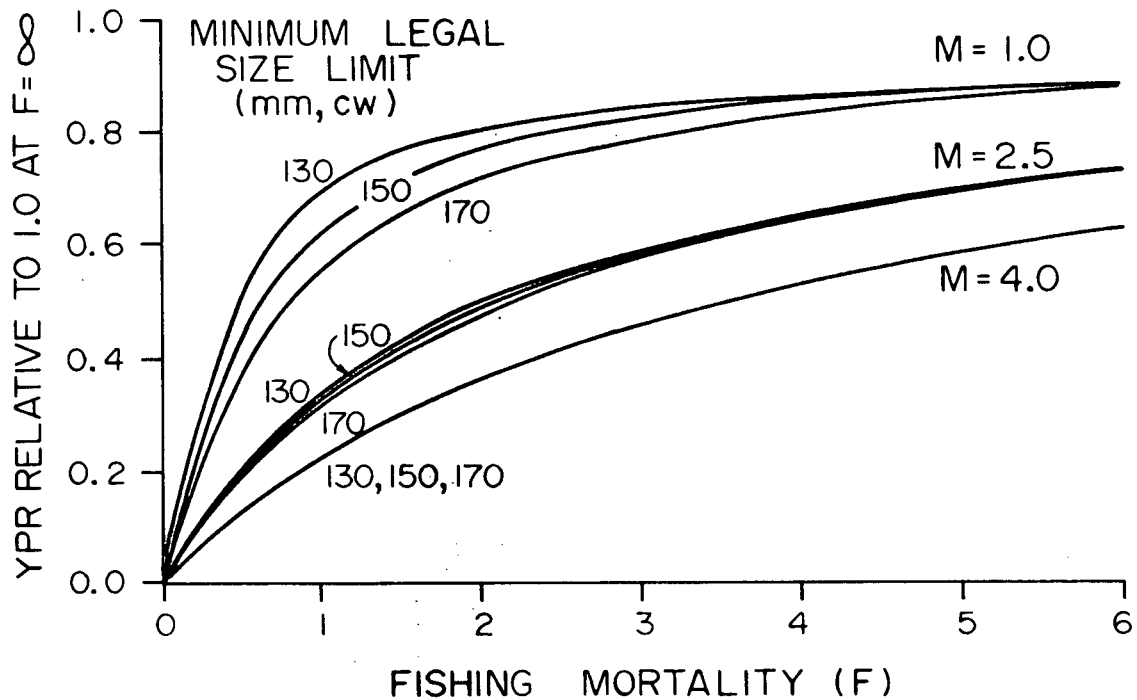


Figure 5.2.2. Yield-per-recruit (YPR) for increasing fishing mortality (F). The results are reported relative to  $F=\infty$ .



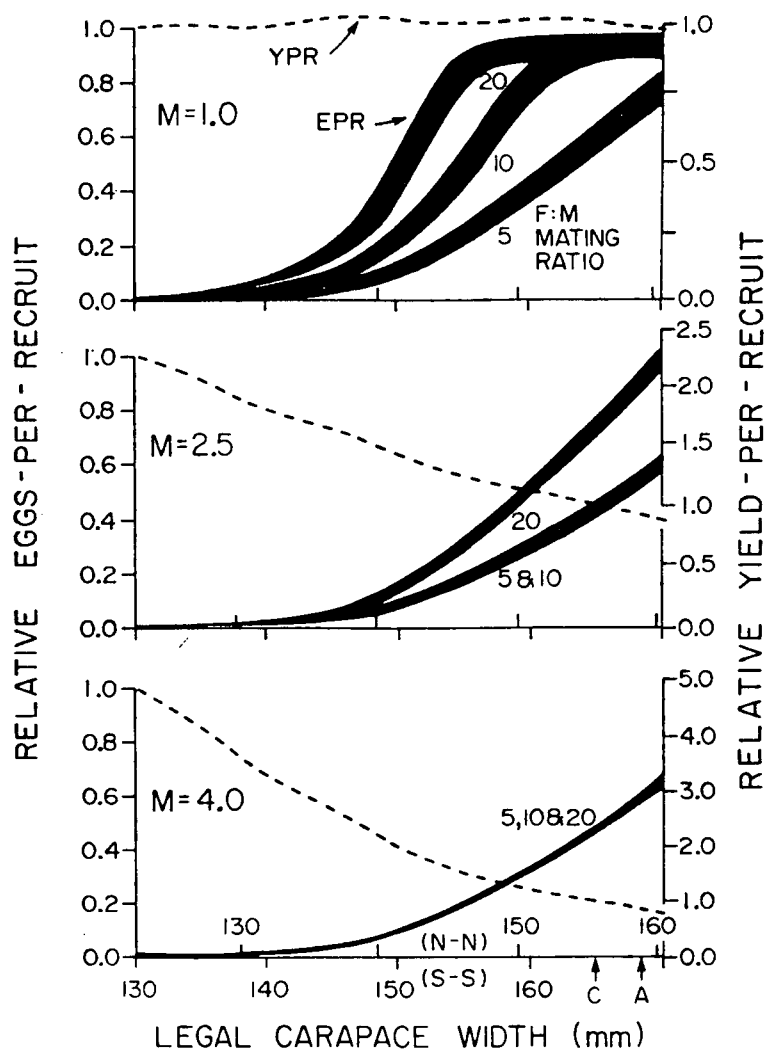


Figure 5.2.3. Yield-per-recruit is reported relative to 1.0 at 165 mm CW (S-S). Eggs-per-recruit are reported relative to an unfished population. The breadth of the relationships indicate the range when the annual decrease in egg production by females that did not mate and moult in previous years is varied from 0.0-1.0 times the egg production of the previous year. Both notch-to-notch (N-N) and spine-to-spine (S-S) carapace widths, and the current Canadian (C) and American (A) legal sizes, are noted.

## 6 DISCUSSION

### 6.1 TRAP PERFORMANCE EXPERIMENTS

Caddy (1979) outlines many factors to be considered when using trap sampling data as an index of population abundance. These include changes in bait effectiveness, accessibility of the trap to the target species, trap design and retention capabilities, environmental factors, and behavior of the target species. In this study such factors resulted in the size frequency distribution and relative abundance of male and female C. magister in traps to vary over time, with corresponding impacts on the interpretation of relative population density.

Figure 4.7.3.5 (page 65) shows that as soak time increases, abundance within traps increases less rapidly and eventually stabilizes. Thus, using the mean daily catch rate as an index of population abundance is inappropriate if soak times are not standardized among the samples. Such problems with trap sampling data are common for invertebrate fisheries. Bennett (1974) demonstrates a dramatic decrease in catch per trap per day with increasing soak times for Cancer pagurus L. Decreasing catch per trap per day has also been reported by Miller (1983) for crabs and lobsters, and Boutillier (1986) for prawns.

Even for equal soak times, if population densities, or size distributions, differ among the populations sampled, then the trap sampling results may be biased. Interactions between individuals within, and attempting to enter, traps can strongly

influence the densities at which entry and exit from traps are balanced. For crabs it seems that intraspecific interactions are agonistic. Miller (1978, 1979) demonstrated that the catch rate of C. productus was limited by agonistic interactions between crabs within a trap, and those trying to enter that trap. Miller (1980) observed agonistic interactions when trapping C. magister and C. productus. By hauling and emptying one set of traps more often than an equivalent set, without changing the bait, he demonstrated that the traps hauled more often caught more crabs. Williams and Hill (1982) concluded that the presence of a crab in a trap reduced the probability of further captures of the portunid crab Scylla serrata Forskal.

Munro (1974) was one of the first to improve information from trap samples. In his paper on the dynamic interactions between Antillean fish traps and reef fishes he reported that the eventual number of fish in a trap results from a balance in the rates of entry and exit processes. These processes were modified by bait effectiveness, trap design and species behavior. Following Munro's theme, this study measured (1) changes in bait effectiveness over time, (2) the effects of agonistic interactions among C. magister individuals in reducing entry rates into a trap, and (3) the ability of traps to retain C. magister of different sizes. Incorporation of these factors into a model simulating entry and exit rates into and out of traps was successful in improving information from trap samples which experienced different soak times.

Although the standardization model improved the trap sampling data, it did not completely explain the dynamic interactions between C. magister and traps. Uncertainty about the correct formulation for the equation simulating agonistic interactions (Eqn. 4.7.3.3, page 55) is an important uncertainty. Also, environmental considerations such as tides, currents, temperature, and seasonal changes in dynamics were not studied. Differences among baits were not studied, but the fishermen whose traps were sampled used geoduck clam (P. abrupta) almost exclusively. Females were assumed to have the same dynamics as males.

By accepting the results of the standardization model one also assumes that the distribution of virtual entry rates for crabs of different sizes reflects their relative density in the population. If different sizes of crabs move at different rates, some will be less likely to encounter a trap than others, and thus may be undersampled. For example, Miller (1975) observed that immature and female Chionoecetes opilio O. Fabricus were aggregated, whereas mature males were apparently randomly distributed. Further, the standardization model does not consider agonistic interactions among crabs outside a trap, where smaller crabs would be expected to be weak competitors against larger crabs. Miller (1978) observed agonistic interactions between individuals of C. productus around the outside of a trap.

Another consideration is that as soak time increases, information on smaller crabs is lost (Fig. 4.7.3.2, page 62). Thus, when the densities and size frequency distributions of samples with long soak times are standardized, the results for smaller crabs will remain biased. The estimated weight of crabs in the traps for the shorter soak times, which is an important variable in the model, will be underestimated because of this lack of information. The estimates of the crab retention probabilities (see Table 4.7.2.2 on page 47 and associated text) are also less reliable for smaller crabs, mainly because traps are not designed to retain smaller crabs.

The above considerations are not as serious a concern for estimating the virtual entry rates for larger crabs. This is because the weight of crabs within a trap must exceed the weight of a crab entering a trap by at least 5 times before the relative entry rate of crabs into a trap is modified (Fig. 4.7.3.3, page 63). Also, the retention rates for larger crabs are higher and more precisely and confidently estimated. Smaller crabs weigh much less than larger crabs and spend much less time in the traps, so the dynamics of the smaller crabs is not an important factor influencing the dynamic interactions between traps and larger crabs.

For the above reasons, the standardization model used in this study should be used cautiously, particularly when making inferences about smaller crabs, or from samples with long soak times. In this study, no samples were considered when the soak

times were longer than 10 days. Also, for standardized samples to which a size frequency analysis was applied, only that portion of the distribution well sampled was included in the analysis.

This standardization model should not be considered an alternative to using equal and short soak times when possible if the purpose is to measure relative population densities. From Fig. 4.7.3.5 (page 65), which shows how the density and size distribution of C. magister in traps changes over time, it can be seen that the entry rates for each 5 mm CW interval are nearly constant for one and two day soaks in both the 1985 and 1986 experiments. Thus data from short soak times may be satisfactory. One should also consider that development of the standardization model required several weeks of field experimentation and computer analysis. In some circumstances the cost of such an analysis may not be justifiable.

Diamond and Hankin (1985b) compared the selectivities of two sets of C. magister traps, one with escape ports, and one without escape ports. They reported difficulties comparing their relative selectivities because of differences in soak times which they could not control. Part of the difficulty results from their functionally defining selectivity as the combination of several interacting processes, e.g. entry and exit rates, changes in bait effectiveness, and agonistic interactions.

For this study I considered these processes separately, and in particular, I define selectivity as the ability of traps to

retain crabs of different sizes for a specified length of time. This definition is more consistent with the definition used in other types of fisheries, e.g. gill nets, trawls (Pope et al. 1975), and presumably provides a more consistent measurement of selectivity that is less sensitive to factors that vary with time, and subsequently alter trap contents. The retention probabilities presented in Table 4.7.2.2 (page 47) are significantly influenced only by the behavior of the species and trap design.

Others have measured the ability of traps to retain C. magister, but have not presented their results to permit comparison with the results of this study. High (1976a) and Muir et al. (1984) present cumulative escapement over time, not escapement rates, and only distinguish sublegal- and legal-sized males. Such information is useful for evaluating trap designs, but is less applicable in models designed to improve understanding of the dynamic interactions between C. magister and traps.

## 6.2 SPATIAL AND TEMPORAL DISTRIBUTIONS

Small male C. magister appeared to retreat short distances to more sheltered habitat in autumn and winter. This was particularly evident in Fig. 4.11.2b where a large concentration of small males gathered in the protected waters of middle Lemmens Inlet. This concentration dispersed during summer, although the decreased abundance is also due to moulting to legal size and

subsequent capture by fishermen. Others observed, or inferred, similar behavior for C. magister. Stevens and Armstrong (1984) reported that the 1980 year-class in Grays Harbor, Washington, disappeared during the winter of its first year, then reappeared the following spring. Gotshall (1978b) observed movement of sublegal- and legal-sized male C. magister in northern California to deeper water in winter, and a return to shallower water in spring. It is reasonable to surmise that this autumn movement is to avoid rough water during the winter. Returning to shallow, warmer and more productive water during summer would conceivably increase food availability.

Average movement rates for male C. magister of <30 m per day (Fig. 4.11.4, page 94), seem consistent with the results of other studies, and suggest that C. magister populations remain local (Butler 1957, Gotshall 1978b). Except for the apparent seasonal changes in habitat, which involve movement over short distances, no studies suggest directional migratory movements for male C. magister. However, Gotshall (1978b) noted that males seem to move in the direction of prevailing currents. Bennett and Brown (1983) report that most tagged male C. pagurus remained near where they were released in the English Channel.

Females were observed to move from coastal inlets, where the substrate ranged from mud to a mud/sand mix, to the more exposed area in the main channel into the study area where the bottom was mainly sand or a sand/gravel mix. Wild (1980) states that females must be at least partially buried in sandy substrate to



extrude and incubate eggs. Stevens and Armstrong (1984) noted that egg-bearing females were rare in Grays Harbor, and speculated that most mature females left the harbour to release their eggs in a preferred environment.

Diamond and Hankin (1985a) argue that mature female C. magister undergo limited movements in offshore waters and suggest that females constitute localized populations. In this study average movement rates for females (<20 m per day) were less than the rates for males (Fig. 4.11.4, page 94). Thus, it appears that females may undergo some migratory movement in order to locate substrate suitable for incubating eggs. They also suspect that females return short distances to shallower water in spring to mate and moult. Males and females may improve mating opportunities by concentrating in shallow water.

Similar movement behavior has been reported for other crabs. Hyland et al. (1984) observed the movement of female portunid crabs, S. serrata, from an estuarine environment, where they lived as juveniles, to the open ocean where they released their eggs. Some females returned to inshore waters after the hatching season. Bennett and Brown (1983) demonstrated that female C. pagurus undergo extensive movements, apparently to habitat more suitable for egg incubation. Using SCUBA, Howard (1982) observed egg-bearing female C. pagurus congregated in relatively deep (24 m), calm water. Since they were rare elsewhere, he

concluded this was a preferred habitat. Dinnel et al. (1987) observed female C. magister in a similar habitat in Puget Sound, Washington, from the submersible PISCES IV.

### 6.3 GROWTH AND MORTALITY

Butler (1961) determined that male C. magister in Dixon Entrance attained legal size during their fourth year after settlement. Using the size frequency analysis of MacDonald and Pitcher (1979), Warner (1985, 1987) concluded that for the two year-classes he followed in northern California, 60% and 28% of each year-class attained legal size (159 mm CW) during their fourth year after settlement. The remainder recruited to the fishery during their fifth year. In this study about 50% of male crabs that moulted into the 155.0 mm instar during their fourth year attained legal size (153.7 mm CW). Since <10% of sublegal-sized males in the 155.0 mm instar will ever attain legal size due to high natural mortality, >90% of the yield from this instar is from males in their fourth year.

Differences in the size frequency models between this and Warner's study are possible reasons for different conclusions about the age when males enter the fishery. With growth structure (i.e. moult increments-at-size) included in the size frequency model in this study (see Schnute and Fournier 1980), the size frequency analysis will tend to define size frequency modes that respect the expected differences in instar mean sizes. Warner's model did not include information on moult increments-

at-size, and further, his analysis did not account for the effect of exploitation of legal-sized males on size frequency distributions. These considerations alone may lead to different interpretations of size frequency information. Nevertheless, unusually high population abundance near Tofino in 1986 (see below, and Fig. 2.2, page 10) may have resulted in high density-dependent mortality. Therefore, male mortality rates may be lower for the population that Warner studied, increasing survivorship and recruitment to the fishery of males older than four years.

Differences in growth rates may also result in differences in the ages at which males recruit to the fishery between British Columbia and California. Stevens and Armstrong (1984) demonstrated that first year C. magister grew more quickly in Grays Harbor estuary, Washington, than in the adjacent open ocean where sea water temperatures were lower. Water temperatures in the inlets near Tofino were slightly higher than along the open coast, so growth rates may be faster. However, it is elucidating to note that there are apparently no large differences in the moult increments-at-size for male C. magister (>80 mm CW) from central California to the Queen Charlotte Islands (Table 4.5.1, page 33).

Butler (1961) and Stevens and Armstrong (1984) determined that females are two years old when they are  $\approx 100$  mm CW. This study suggests that females in the 135.5 mm instar are three years old, thus those in the 149.4 and 161.4 mm instars are

probably four and five years old, given that they undergo an annual moult. However, it has been suggested in this study, and by Hankin et al. (1985), that moults may occur less frequently than annually for females larger than  $\approx 145$  mm CW, particularly in intensively fished populations (Section 4.14). As was observed for males, moult increments-at-size for female C. magister vary little from central California to the Queen Charlotte Islands (Table 4.5.2, page 33).

The exploitation rate on legal-sized male C. magister near Tofino is high ( $F=5.11-6.90$ ), with legal-sized males having only a 50% chance of surviving the fishery for more than 37-50 days. Because of the intensity of the fishery, the seasonal pattern of fishing success in Lemmens Inlet (Fig. 4.9.4, page 76) mimics the time distribution of moulting into legal size for the 128.0 mm instar (Fig. 4.13.3, page 105). Moulting occurs over 6-9 months sustaining the fishery for most of the year. Figure 4.9.5 (page 77), which presents a seasonal profile of virtual entry rates of legal-sized males (i.e. standardized data) for traps samples from throughout the study area, shows a pattern similar to that in Fig. 4.9.4. The seasonal pattern of fishing success observed within Lemmens Inlet (Fig. 4.9.4) was not apparent outside Lemmens Inlet, apparently because less effort (lower trap densities and longer soak times) disguised the relationship between moult timing and catch rates ( $n \cdot \text{trap}^{-1} \cdot d^{-1}$ ).

High fishing mortality rates have previously been measured for C. magister in northern California. Jow (1965) estimated  $F$  at 7.9, based on recovery of tagged legal-sized males during the fishing season, which lasts about six months. Using catch-per-unit-effort data, Gotshall (1978a) estimated  $F$  to range from 1.18-7.00, depending on the year. Similarly, Methot and Botsford (1982) estimated  $F$  to range from 0.8-3.2 for the period 1951 until 1977.

Natural mortality for male C. magister in the 155.0 mm instar was determined to be high. A maximum estimate of  $M=3.48$  was suggested by the disappearance of tagged sublegal-sized males over time (Table 4.13.1, page 97 and Fig. 4.13.1, page 103). Estimates of  $M$  ranging from 2.87-4.37 were suggested by the lack of recovery of legal-sized males that were tagged when they were sublegal size (Table 4.13.5, page 102). An estimate for  $M$  of 4.33-4.48 was suggested from the recovery of males released and recovered when legal size. No detection of the 183.8 mm male instar in size frequency analyses, including those performed on the lightly fished Holberg Inlet fishery, also strongly suggests low survivorship to instars larger than the 155.0 mm instar.

Table 4.13.5 shows that males have a reduced likelihood to survive to the next instar as their size increases. The catch curves in Fig. 4.14.1 (page 110) indicate the same phenomenon for females. Increasing natural mortality rates with increasing size have been observed for other crab species. Hill (1975) reports an increase in the mortality rate of the portunid crab,

S. serrata, from its second to third year of life. As crabs become larger, and the energy required to attain the next instar increases, the time between moults increases. Coupled with shell deterioration, and increasing energy requirements, the likelihood of these individuals attaining the next instar is decreased.

The growth and mortality rate estimates for males obtained in this study may have implications for models which have attempted to explain C. magister population dynamics in other fisheries. In particular, models proposed to explain the cyclical nature of C. magister landings in California (see McKelvey et al. 1980, Botsford 1984, 1986a, Methot 1986) have been based on male growth rates slower (e.g.  $\approx 50\%$  of males becoming legal size when 5+ years old), and mortality rates much lower ( $M=0.15-0.90$  for immature males), than those presented here. If the growth and mortality rates obtained in this study for mature males can be justified for immature males in populations along the coast of Washington, Oregon and California, these models may need to be adjusted numerically, and in some cases, perhaps conceptually.

Conceivably the high mortality rates obtained in this study are partly due to density-dependent factors resulting from an unusually high abundance of C. magister in 1986. Cancer magister landings for SA 24 in 1986 were 265 t. This is the third highest total in the history of the fishery, and more than double the mean tonnage landed the previous 10 years ( $131 \pm 26$  t, see Fig. 2.2, page 10). However, size frequency analysis on males in

other British Columbia fisheries also indicated low survivorship of sublegal-sized males from the 155.0 mm instar to the 183.8 mm instar. Variation in  $M$  is a reasonable expectation since Gotshall (1978b), using catch-per-unit-effort data, estimated  $M$  to range from 0.88-2.50 in northern California. However, Gotshall's estimates of mortality and population size were not obtained independently, his estimates of population size (Leslie method, see Ricker 1975) failing the assumption of low natural mortality. For this reason his estimates of  $M$  cannot be accepted with confidence.

Male crab densities near Tofino in 1987 appear to be considerably lower than in 1986, as indicated by low pre-recruit abundance and declining fishing success (G.S. Jamieson, Pacific Biological Station, Nanaimo, B.C., pers. comm.). This may provide an opportunity to measure the effect of density on mortality, facilitating more reliable extrapolations to habitats with different crab densities.

The life history of C. magister, as currently understood, appears typical of r-strategists (Stearns 1976, 1977): fast growing, short-lived, high fecundity, early maturity, and fluctuating population sizes. Associated with these traits is the prediction of high density-independent mortality. Causes of a high natural mortality rate for C. magister are presently unknown. Unlike many invertebrate species whose juvenile and adult stages occupy different habitats (Caddy 1986), juvenile and adult C. magister occur together on sand, so density-dependent

mortality may be important for this species. For example, cannibalism of adults on juveniles (Botsford and Wickham 1978) is being investigated as a possible explanation of the cycles in California C. magister landings.

Factors associated with the growth, physiology, and life history of C. magister individuals are possible causes of density-independent mortality. Over the course of this study crabs showed an obvious progression of shell deterioration and loss of vigor as the time they spent within an instar increased.

Disease is not believed to be an important contributor to C. magister mortality near Tofino but predation is a possibility. The giant Pacific octopus, Octopus dofleini (Wulker), an important predator of C. magister, is abundant in this vicinity (High 1976b, Hartwick et al. 1978). Octopus dofleini were occasionally caught in crab traps during this study. High (1976a) observed O. dofleini predation on C. magister during trap escapement experiments.

#### 6.4 YIELD- AND EGGS-PER-RECRUIT

Males under legal size in the 155.0 mm instar (about 50% of this instar) have a low probability (<10%) of attaining legal size at a future date. Figure 5.2.3 (page 122) shows that for  $M=2.5-4.0$  (similar to the estimates obtained in Section 4.13) there is a potential increase in yield-per-recruit of 2-3 fold relative to the current minimum legal size limit of 165 mm CW (spine-to-spine) if all males >140 mm CW (spine-to-spine) are



exploited. Further reductions in the size limit also suggest increased yield, but presume accuracy in the model results below the carapace widths for which mortality was confidently measured.

For many species yield-per-recruit cannot be improved by reducing the size of animals taken in a fishery because of the risk of recruitment-overfishing (Cushing 1973), i.e. reducing population egg production below a level that can be consistently compensated by density-dependent responses, thereby resulting in declining abundance. For C. magister a relationship between stock and recruitment has not been found. In fact, documentation of compensatory stock and recruitment relationships is rare for invertebrates in general (Hancock 1973, Caddy 1986). As Jamieson (1986) notes, such reliable relationships may or may not exist for certain crab species, and in many cases relationships may be disguised by poor data. Consequently, many invertebrate fisheries are managed by size limitations which protect reproductive females. Minimum legal size limits have been successful measures in some fisheries, e.g. the eastern Canadian lobster (H. americanus) fishery, where regulatory measures apparently protect a sufficient portion of population egg production (Jamieson and Caddy 1986).

The possibility of recruitment-overfishing for C. magister populations has never been seriously considered because of the historical presumption that the current Canadian and American minimum legal size limits for males preserve adequate population egg production (Cleaver 1949, Poole and Gotshall 1965, Methot

1986)). Since few females attain legal size, and egg bearing females of all observed sizes above the size-at-maturity are relatively common, it has been assumed that taking only males did not affect population egg production. In support of this, British Columbia fisheries show no strong evidence of recruitment-overfishing.

In apparent agreement with this assumption, this study noted that all mature females (greater than  $\approx 115$  mm CW) dissected in the field contained a pair of sperm packs. However, the female catch curves in Fig. 4.14.1 (page 110), which imply decreasing likelihoods of females attaining larger instars in the more heavily fished regions, suggest that mature females may only moult when accompanied by a larger male in a mating embrace. It is typical for female cancrid crabs to mate with a larger and hard-shelled male (Butler 1960, Snow and Neilsen 1966, Elner et al. 1985). Figure 4.4.1 (page 31), which plots the relative sizes of males and females in mating embraces, suggests that females larger than  $\approx 140$  mm CW may not have an opportunity to mate and moult in the more heavily fished populations.

Such a phenomenon of females moulting only when accompanied by a male in a mating embrace is consistent with the observation that all mature females contained a pair of sperm packs. It is noteworthy, however, that Brown and Bennett (1980) suggested that large female C. pagurus failed to undergo an annual moult because the presence of a pair of sperm packs inhibited moulting. One

can not interpret from their results whether the moulting of females may have been inhibited by the absence of males large enough to mate with the larger females.

So even though all females in a heavily fished population may have been mated, population egg production may still be reduced relative to an unfished population. This would result from (1) a shift in the size frequency distribution of females to smaller sizes, with smaller females producing fewer eggs than larger females (Eqn. 5.1.1 on page 116 of this study, which is from Hankin et al. 1985), and (2) reduced fecundity each year a female fails to moult. Both result from a decrease in potential matings by the male population.

In an intense C. magister fishery many legal-sized males landed are soft-shelled. From a reproductive perspective, landing a soft-shelled male that is just legal size (at the mode of the 155.0 mm instar) is equivalent to landing a hard-shelled male 128 mm CW (at the mode of the next smaller instar). In consideration of the size frequency distribution of the percent of males with mating marks (Fig. 4.10.1, page 81), it is likely that many males will have never mated before being taken by the fishery. Therefore, in an heavily exploited regional fishery, virtually all mating is by sublegal-sized males in the 155.0 mm instar.

Intense fishing results in the number of potential matings by males being reduced by  $\approx 50\%$  relative to an unfished

population. The actual decrease in the number of matings depends on how well sublegal-sized males compensate by mating more females than they would in an unfished population. Figure 5.2.1 (page 120) indicates that as the potential F:M mating ratio for the male population increases above  $\approx 10:1$  (for  $M=2.5$ ), the impact on population egg production decreases. The implication is that an F:M mating ratio  $>10:1$  includes surplus mating potential which can buffer mating potential lost due to fishing.

The eggs-per-recruit analysis in this study, which modeled the male and female reproductive processes, suggests that high exploitation of males above the current minimum legal size limit might reduce eggs-per-recruit by up to 50% relative to an unfished population. In consideration of this conclusion, the possibility of recruitment-overfishing in heavily exploited fisheries should be reinstated as a concern for fisheries managers.

Full confidence in the eggs-per-recruit model requires a more complete understanding of reproductive behavior. The model presented in this study is based on best estimates, and uncertainty in these estimates, of important population variables. Like most attempts to simulate natural processes there are uncertainties in (1) the numerical representation of processes which are generally understood, but are difficult to quantify, and (2) in the conceptual understanding of natural processes. In this analysis the important numerical uncertainty is the F:M mating ratio, and in particular the functional

response of the F:M mating ratio to female density. The important conceptual uncertainty concerns female moulting frequency and its relationship to the availability of males for mating.

Reproductive biology (e.g. age-at-maturity, fecundity, seasonality of egg hatching) has been described for many crab species but information on reproductive behavior in nature (e.g. F:M mating ratios, duration of mating activity, female moulting pattern) is more elusive and remains poorly understood for crustaceans in general. Increased knowledge of reproductive behavior is not only important for understanding the population dynamics of C. magister, but may contribute to explanations of the recent sharp declines in landings of the red king crab (Blau 1986) and the Atlantic snow crab (Elner and Bailey 1986).

With regard to the present study, there is insufficient information to adequately debate whether a female with a pair of sperm packs does, or does not, moult annually. Using relative egg production as a measure of fitness (Stearns 1976, 1977), the better reproductive strategy is the one that produces the most viable eggs in the future. If mating, moulting and producing a larger clutch of eggs is a higher risk for a female, in terms of future population egg production, than not moulting and producing fewer eggs, then the suggestion of Brown and Bennett (1980) that females do not moult if they have a pair of sperm packs is the more favourable evolutionary argument. If mating and moulting has the lower risk, then the more favourable argument is that

females should not moult without mating. Uncertainty about which life history is the correct explanation for C. magister influences how biological information (e.g. female catch curves, Fig. 4.14.1, page 110) is interpreted. This can have important implications for management of the species.

With our current understanding of male and female growth and mortality, there seems to be no natural circumstance when females are deprived of males suitable for mating. So, in an unfished population a female can expect to be mated, and therefore should not moult without mating since, considering the high natural mortality, she has little chance of surviving to mate and moult the following year. In this circumstance, the more fit female, in terms of future egg production, is the one that delays moulting until a suitable mate is found. The consequence of this strategy in a heavily fished population would be a shift in the female size frequency distribution to smaller sizes.

Understanding natural reproductive behavior requires a knowledge of the physiological interactions between mating males and females, and the factors that control mating. The physiological argument for brachyuran crabs in general is that a female secretes a pheromone to attract males when she is preparing to moult (Hartnoll 1969, Christy 1987). Once a suitable mate is found, the mating ritual and subsequent mating occur. For 'female centered competition', which is the label Christy (1987) applies to the mating behavior of Cancer spp., this means that males competitively search and aggressively

defend their female partners for a few days before, and perhaps after, the actual mating. There is strong evidence of the release of a pheromone to attract males for a few portunid crabs (Christy 1987), and Edwards (1966) suggested this may also occur for C. pagurus. There is some indirect evidence that cancrid females release a water-borne pheromone in their urine in the days prior to moulting (Christy 1987), but there is no proof that a mating pheromone exists for any brachyuran crab species.

It is critical that we understand the reproductive physiology of C. magister, and determine if the endocrinology of moulting and reproduction is different for females with and without sperm packs. It needs to be explained why population information suggests females do not moult if suitable males are not available, yet mature females with sperm packs have been observed to moult in the absence of males in laboratory tanks. Also, the suggestion of Brown and Bennett (1980) that female C. pagurus with sperm packs do not moult does not explain how females with sperm packs attain the larger instars. In this study, all mature C. magister females, of all sizes, had sperm packs.

An 'experimental management' approach (Walters and Hilborn 1978, Hilborn and Walters 1981), where the F:M mating ratio is deliberately altered by varying the minimum legal size limit for males, and prohibiting the landing of females, would also help improve our understanding of C. magister reproduction dynamics. Some questions regarding reproductive behavior can be addressed

only by experimentation at this scale (Walters 1986). For example, experiments to test for possible changes in female population structure resulting from harvesting males above a relatively low minimum legal size limit, thereby eliminating mating opportunities, cannot be performed in a laboratory. Without large scale experimentation one cannot be certain that the relationship observed between the degree of exploitation of males and the absence of larger females (Section 4.14) is 'cause and effect.

An ideal location would be a small, intensely exploited fishery with an exogenous larval supply. Such a location would ensure that larval recruitment to the population would not be affected by experimental treatments. The site of the present study near Tofino (SA 24) apparently meets these criteria since Jamieson and Phillips (in press) suggest that larvae settling near Tofino are unlikely to have hatched from local females. They are more likely to have been hatched from females from along the coast of Washington, Oregon, California or northern British Columbia.

The basis of such an experiment would involve removing males above a minimum legal size limit considerably lower than the current minimum legal size limit of 165 mm CW (spine-to-spine) from a C. magister population. Figure 5.2.3 (page 122) suggests a minimum legal size limit of 140 mm CW (spine-to-spine) might increase yield-per-recruit by a factor of three (at  $M=4.0$ ). If such an experiment were implemented in SA 24, increased



yield-per-recruit might be evident in future landing statistics. The high annual exploitation rate near Tofino, of essentially a single year-class, suggests landing statistics may reflect population abundance.

If exploiting males above a minimum legal size limit of 140 mm CW (spine-to-spine) denies females an opportunity to mate and moult, then with a high exploitation rate this should also result in very few females >120 mm CW being mated (See Fig. 4.4.1, page 31). Consequently, a shift in female size frequency distributions to smaller sizes should occur with few females attaining sizes much larger than one moult increment greater than  $\approx 120$  mm CW. There is a high quality data base for assessing trends in female size frequency distributions over time, since the Dungeness crab fishery near Tofino has been sampled extensively since 1985.

An increase in yield resulting from lowering the minimum legal size limit to 140 mm CW near Tofino might be detected using a time series step intervention analysis (Noakes 1986) on the landing statistics from SA 24. For example, a three fold increase in SA 24 landing statistics post-1986 over the mean tonnes landed from 1954-1986, while maintaining the variance proportional to the pre- and post-intervention means, should be statistically detected in only a few years. Intervention analysis on 50 sets of simulated data for years post-1986 recognized a significant ( $\alpha=.05$ ) increase in tonnes landed after one year in 39 cases. For the remaining 11 cases a significant

increase was detected in five years or less. Obviously, less dramatic increases would take longer to detect. Landings would have had to exceeded 433 t in 1987 for a significant increase over landings prior to 1987 to be detected in 1987. The reader is referred to Lettenmaier et al. (1978) who tested the power of time series intervention analyses for detecting perturbations to systems, and who provide guidelines regarding data requirements.

There are obvious managerial and political difficulties in implementing an experiment where the minimum legal size limit is lowered. With all regional fisheries in British Columbia being open year round (with exceptional closures to protect soft-shelled males), enforcement of larger size limits in contemporaneous fisheries in regions other than SA 24 could be difficult. Initially it would be very difficult to convince fishermen that the Tofino area is perhaps the only region biologically suited to this type of management experiment. Then later, if the experiment is successful, it will be perhaps more difficult to tell them that they cannot benefit from this new knowledge because of concerns about the relationship between stock and recruitment.

Marketing smaller crabs is not anticipated to be a problem since buyers seem to be more interested in landed volume than crab size. This is particularly true for buyers of crabs to be shucked for their meat. However, allowing males as small as 140 mm CW (spine-to-spine) to be landed could result in fishermen requesting changes in regulations governing the size of escape

ports. Currently each trap must have at least one circular escape port with an inside diameter of not less than 100 mm. From Table 4.7.2.2 (page 47) it can be seen that Traps B and D, which are fished commercially near Tofino, have poor retention capabilities for crabs <145 mm CW. Issues such as this which require interventions by fishery managers tend to lessen the likelihood of experiments of this scale being implemented.

## 6.5 SUMMARY

In conclusion, the main findings of this study of C. magister population dynamics near Tofino, B.C. are:

1. Males in the  $102.9 \pm 9.8$  mm instar, which dominated in the summer two years after settlement, moulted twice during the following 1.5 years to attain the  $155.0 \pm 11.2$  mm instar, the first instar with legal-sized males. A mark-recovery program, and size frequency analysis on commercial trap samples standardized to correct for differences in soak time, showed that the 155.0 mm instar began to form during the spring, three years after settlement, and continued to form throughout the remainder of the year. The size frequency distribution of males with mating marks (Butler 1960) suggested that most males are not sexually active before attaining the 155.0 mm instar.

2. Females reach sexual maturity in the  $100.7 \pm 12.8$  mm instar during the summer two years after settlement. They first mate near this size and produce eggs the following winter while in the

119.4±11.0 mm instar. They appear to moult annually after this instar, the bulk of the moulting occurring during the summer months when mating activity is high.

3. There appear to be only small differences in the moult increments-at-size for male and female C. magister from California to the Queen Charlotte Islands. It could not be ascertained if these differences are biological or due to differences in measurement.

4. Natural mortality of males was estimated to be high. (Female natural mortality was not estimated). The annual instantaneous rate of natural mortality (M) was estimated at 2.87-4.48 for males mainly in the 155.0 mm instar. The data suggest that the mortality rate may increase as the time a male spends within an instar increases, and that the mortality rate during or shortly after a moult is higher than the intermoult mortality.

5. Movement, as determined by mark-recovery methodology, was judged not to be extensive. Most males and females moved, on average, <30 m per day. There was evidence that males retreat to deeper water during the winter, perhaps to avoid rough water, and then return to shallower water the following spring. Maturing females were observed to move from the coastal inlets to the more exposed coast, perhaps to incubate and release their eggs in a preferred environment.

6. The fishery near Tofino is composed mainly of males greater than the minimum legal size limit of 154 mm CW in the 155.0±11.2 mm instar. About 50% of the males in this instar enter the fishery during their fourth year after settlement. There remains some uncertainty about the proportion of this age-class which recruits during its fourth year. Due to high natural mortality, this study determined that less than 10% of sublegal-sized males that attained the 155.0 mm instar during 1985 survived to enter the fishery the following year. However, a study in California (Warner 1985, 1987) suggests a greater percentage of legal-sized males may be caught when older than four years.

7. The annual instantaneous rate of fishing mortality (F) of legal-sized males, as determined from a mark-recovery program, was estimated at 5.11-6.90. This indicates an annual survival from fishing of <1%. Size frequency analysis on commercial trap samples standardized to correct for differences in soak times confirmed a very high degree of exploitation (≈60-100%) of legal-sized males. In consideration of the high natural mortality of sublegal-sized males in the 155.0 mm instar, landing statistics from SA 24 may reflect population abundance and year-class strength.

8. Size frequency and abundance information from commercial trap samples changes with increasing soak time. Differences in soak times for otherwise replicate trap samples produce biases caused by (1) the dynamics of entry and exit over time, (2)

changes in bait effectiveness over time, and (3) agonistic interactions between crabs within a trap and crabs attempting to enter that trap. Several experiments were performed which measured these processes. The results of these experiments were used to improve the trap sampling data by correcting for the effects of different soak times.

9. Yield-per-recruit analysis indicated that the current minimum legal size limit of 165 mm CW (spine-to-spine) is well above the size limit optimizing yield. For example, lowering the minimum legal size limit to 140 mm CW (spine-to-spine) may result in about a three fold increase in yield-per-recruit. If this lower size limit is tested experimentally in the regional fishery near Tofino, the hypothesized improvement is large enough that increased landings may be statistically detected by time series analysis of annual landings in less than five years. The fishery near Tofino is argues to be an excellent location to perform such an experiment.

10. Data on the carapace widths of males and females forming mating pairs permitted a quantitative estimate of the size of male required by a female in a mating embrace. The results suggested females larger than  $\approx 140$  CW would have difficulty finding a male partner in heavily exploited fisheries since males greater than the minimum legal size limit of 154 mm CW would be rare. Since females moult when mating, this might result in growth stagnation at instars smaller than would otherwise be attained.

11. All females greater than  $\approx 115$  mm CW that were dissected in this study contained a pair of sperm packs placed in their spermathecae by a male during mating. In consideration of the relative sizes of mating pairs, such results strongly suggest that no females attain larger instars without having mated with a larger male. Large males may not be available in an intensely fished population. Commercial trap samples from four regional fisheries which experienced light to heavy fishing supported this interpretation. Large females were most abundant in the lightly fished region and least abundant in the most heavily fished region.

12. Eggs-per-recruit analysis indicated that in an intense fishery population egg production may be reduced by up to 50% relative to an unfished population. This results from (1) a shift in female size frequency distributions to smaller sizes due to growth stagnation from a lack of males of a size suitable for mating, (2) smaller females producing fewer eggs, and (3) reduced fecundity each year a female fails to mate and moult. There is no strong evidence of recruitment-overfishing in British Columbia C. magister fisheries, but I recommend that managers of C. magister fisheries reconsider the historical presumption that the current Canadian and American minimum legal size limits provide adequate protection of population egg production. It is important to distinguish if populations are maintained by the protection of egg production or by compensatory density-dependent mortality in early life history stages.

## 7 LITERATURE CITED

- Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control AC-19: 716-723.
- Armstrong, D.A., and D.R. Gunderson. 1985. The role of estuaries in Dungeness crab early life history: A case study in Grays Harbor, Washington, p. 145-169. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Atema, J., and J.S. Cobb. 1980. Social behavior, Chapter 8, p. 409-450. In J.S. Cobb and B.F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Physiology and behavior. Academic Press, Toronto, Canada. 463 p.
- Barry, S. 1985. Overview of the Washington coastal Dungeness crab fishery, p. 33-36. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Bennett, D.B. 1974. The effects of pot immersion time on catches of crabs, Cancer pagurus L. and lobsters Homarus gammarus (L.). J. Cons. Int. Explor. Mer. 35: 332-336.
- Bennett, D.B., and C.G. Brown. 1983. Crab (Cancer pagurus) migrations in the English Channel. J. Mar. Biol. Assoc. U.K. 63: 371-398.
- Blau, S.F. 1986. Recent declines of red king crab (Paralithoides camtschatica) populations and reproductive conditions around the Kodiak archipelago, Alaska, p. 360-369. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Botsford, L.W. 1984. Effect of individual growth rates on expected behavior of the northern California Dungeness crab (Cancer magister) fishery. Can. J. Fish. Aquat. Sci. 41: 99-107.
- Botsford, L.W. 1986a. Population dynamics of the Dungeness crab (Cancer magister), p. 140-153. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Botsford, L.W. 1986b. Effects of environmental forcing on age-structured populations: northern California Dungeness crab (Cancer magister) as an example. Can. J. Fish. Aquat. Sci. 43: 2345-2352.



- Botsford, L.W., and D.E. Wickham. 1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (Cancer magister) fishery. J. Fish. Res. Board Can. 35: 833-843.
- Botsford, L.W., R.D. Methot Jr. and W.J. Johnston. 1983. Effort dynamics of the northern California Dungeness crab (Cancer magister) fishery. Can. J. Fish. Aquat. Sci. 40: 337-346.
- Botsford, L.W., R.D. Methot and J.E. Wilen. 1982. Cyclic covariation in the California king salmon, Oncorhynchus tshawytscha, silver salmon, O. kisutch, and Dungeness crab, Cancer magister, fisheries. Fish. Bull. 80: 791-801.
- Boutillier, J.A. 1986. Fishing effort standardization in the British Columbia prawn (Pandalus platyceros) trap fishery, p. 176-181. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Boyce, W.E., and R.C. DiPrima. 1977. Elementary differential equations and boundary value problems. Third Edition. John Wiley and Sons, Toronto, Canada. 582 p. plus Appendices.
- Brown, C.G., and D.B. Bennett. 1980. Population and catch structure of the edible crab (Cancer pagurus) in the English Channel. J. Cons. Int. Explor. Mer. 39: 88-100.
- Butler, T.H. 1957. The tagging of the commercial crab in the Queen Charlotte Islands region. Fish. Res. Board Can. Pac. Prog. Rep. 109: 16-19.
- Butler, T.H. 1960. Maturity and breeding of the Pacific edible crab, Cancer magister Dana. J. Fish. Res. Board Can. 17: 641-646.
- Butler, T.H. 1961. Growth and age determination of the Pacific edible crab Cancer magister Dana. J. Fish. Res. Board Can. 18: 873-889.
- Caddy, J.F. 1979. Some considerations underlying definitions of catchability and fishing effort in shellfish fisheries, and their relevance for stock assessment purposes. Fish. Mar. Ser. MS Rep. 1489: 18 p.
- Caddy, J.F. 1986. Modelling stock-recruitment processes in Crustacea: some practical and theoretical perspectives. Can. J. Fish. Aquat. Sci. 43: 2330-2344.

- Campbell, A. 1986. Implications of size and sex regulations for the lobster fishery of the Bay of Fundy and southwestern Nova Scotia, p. 126-132. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Christy, J.H. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. Bull. Mar. Sci. 41: 177-191.
- Cleaver, F.C. 1949. Preliminary results of the coastal crab (Cancer magister) investigation. Wash. Dep. Fish. Biol. Rep. 49A: 47-82.
- Collier, P.C. 1983. Movement and growth of post-larval Dungeness crabs, Cancer magister, in the San Francisco area, p. 125-133. In P.W. Wild and R.N. Tasto [ed.] Life history, environment and mariculture studies of the Dungeness crab, Cancer magister, with emphasis on the central California fishery resource. Calif. Dep. Fish and Game Fish Bull. 172.
- Cushing, D.H. 1973. Dependence of recruitment on parent stock. J. Fish. Res. Board Can. 30: 1965-1976.
- Demory, D. 1985. An overview of Oregon Dungeness crab fishery with management concepts for the future, p. 27-32. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Diamond, N. 1983. Demographic statistics and annual molting probabilities of the adult female Dungeness crab (Cancer magister) in northern California. Masters thesis, Humbolt State University, Arcata, California 106 p.
- Diamond, N., and D.G. Hankin. 1985a. Movements of adult female Dungeness crabs (Cancer magister) in northern California based on tag recoveries. Can. J. Fish. Aquat. Sci. 42: 919-926.
- Diamond, N., and D.G. Hankin. 1985b. Biases in crab tag recovery data, p. 341-356. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Dinnel, P.A., D.A. Armstrong, R.R. Lauth and G.S. Jamieson. 1987. Use of the PISCES IV submersible for determining the distributions of Dungeness crab, shrimp, and bottomfish in Port Gardner, Washington. Univ. Wash., Fish. Res. Inst. Final Rep. FRI-UW-8709. 16 p.
- Edwards, E. 1966. Mating behavior in the European edible crab (Cancer pagurus L.). Crustaceana 10: 23-30.

- Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. SIAM, Monogr. No. 38, CBMS-NSF.
- Elner, R.W., C.A. Gass and A. Campbell. 1985. Mating behavior of the Jonah crab, Cancer borealis Stimpson (Decapoda, Brachyura). Crustaceana 48: 34-39.
- Elner, R.W., and R.F.J. Bailey. 1986. Differential susceptibility of Atlantic snow crab, Chionoecetes opilio, stocks to management, p. 335-346. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Fogarty, M.J., and S.A. Murawski. 1986. Population dynamics and assessment of exploited invertebrate stocks, p. 228-244. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Gotshall, D.W. 1978a. Catch-per-unit-of-effort studies of northern California Dungeness crabs, Cancer magister. Calif. Fish and Game 64: 189-199.
- Gotshall, D.W. 1978b. Northern California Dungeness crab, Cancer magister, movements as shown by tagging. Calif. Fish and Game 64: 234-254.
- Gulland, J.A. 1983. Fish Stock Assessment. A manual of basic methods. FAO/Wiley Series on Food and Agriculture. John Wiley and Sons, Toronto, Canada. 223 p.
- Gunderson, D.R., D.A. Armstrong and C. Rogers. 1985. Sampling design and methodology for juvenile Dungeness crab surveys, p. 135-144. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Hancock, D.A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P-V. Reun. Cons. Int. Explor. Mer. 164: 113-131.
- Hankin, D.G., N. Diamond, M. Mohr and J. Ianelli. 1985. Molt increments, annual molting probabilities, fecundity and survival rates of adult female Dungeness crabs in northern California, p. 189-206. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Hartnoll, R.G. 1969. Mating in the Brachyura. Crustaceana 16: 161-181.
- Hartwick, E.B., P.A. Breen and L. Tulloch. 1978. A removal experiment with Octopus dofleini (Wulker). J. Fish. Res. Board Can. 35: 1492-1495.

- High, W.L. 1976a. Escape of Dungeness crabs from pots. Mar. Fish. Rev. 38(4): 18-23.
- High, W.L. 1976b. The giant Pacific octopus. Mar. Fish. Rev. 38(9): 17-22.
- Hilborn, R., and C.J. Walters. 1981. Pitfalls of environmental baseline and process studies. Environ. Impact Assess. Rev. 2: 265-278.
- Hill, B.J. 1975. Abundance, breeding and growth of the crab Scylla serrata in two South African estuaries. Mar. Biol. 32: 119-126.
- Hipel, K.W., and A.I. McLeod. 1987. Applied Box-Jenkins modelling for water resources and environmental engineers. Elsevier, Amsterdam. (In press)
- Howard, A.E. 1982. The distribution and behavior of ovigerous edible crabs (Cancer pagurus), and consequent sampling bias. J. Cons. Int. Explor. Mer. 40: 259-261.
- Hyland, S.J., B.J. Hill and C.P. Lee. 1984. Movement within and between different habitats by the portunid crab Scylla serrata. Mar. Biol. 80: 57-61.
- Jamieson, G.S. 1985. The Dungeness crab, Cancer magister, fisheries of British Columbia, p. 37-60. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Jamieson, G.S. 1986. Implications of fluctuations in recruitment in selected crab populations. Can. J. Fish. Aquat. Sci. 43: 2085-2098.
- Jamieson, G.S., and J.F. Caddy. 1986. Research advice and its application to management of invertebrate resources, p. 416-424. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Jamieson, G.S., and A.C. Phillips 1988. Occurrence of Cancer crab (C. magister and C. oregonensis) megalopae off the west coast of Vancouver Island, British Columbia. Fish. Bull. 86: (In press)
- Johnson, D.F., L.W. Botsford, R.D. Methot Jr. and T.C. Wainwright. 1986. Wind stress and cycles in Dungeness crab (Cancer magister) catch off California, Oregon, and Washington. Can. J. Fish. Aquat. Sci. 43: 838-845.
- Jow, T. 1965. California-Oregon cooperative crab tagging study. Pac. Mar. Fish. Comm., 17th Ann. Rep. for the year 1964, p. 51-52.

- Lettenmaier, D.P., K.W. Hipel and A.I. McLeod. 1978. Assessment of environmental impacts part two: data collection. Environ. Manage. 2: 537-554.
- MacDonald, P.D.M., and T.J. Pitcher. 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. 36: 987-1001.
- McKelvey, R., D. Hankin, R. Yanosko and C. Snugg. 1980. Stable cycles in multistage recruitment models: an application to the northern California Dungeness crab (Cancer magister) fishery. Can. J. Fish. Aquat. Sci. 37: 2323-2345.
- Methot, R.D. Jr. 1986. Management of Dungeness crab fisheries, p. 326-334. In G.S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- Methot, R.D. Jr., and L.W. Botsford. 1982. Estimated preseason abundance in the California Dungeness crab (Cancer magister) fisheries. Can. J. Fish. Aquat. Sci. 39: 1077-1083.
- Miller, R.J. 1975. Density of the commercial spider crab, Chionoecetes opilio, and calibration of effective area fished per trap using bottom photography. J. Fish. Res. Board Can. 32: 761-768.
- Miller, R.J. 1978. Entry of Cancer productus to baited traps. J. Cons. Int. Explor. Mer. 38: 220-225.
- Miller, R.J. 1979. Saturation of crab traps: reduced entry and escapement. J. Cons. Int. Explor. Mer. 38: 338-345.
- Miller, R.J. 1980. Design criteria for crab traps. J. Cons. Int. Explor. Mer. 39: 140-147.
- Miller, R.J. 1983. How many traps should a crab fisherman fish? N. Am. J. Fish. Manage. 3: 1-8.
- Mittertreiner, A., and J. Schnute. 1985. Simplex: a manual and software package for easy nonlinear parameter estimation and interpretation in fishery research. Can. Tech. Rep. Fish. Aquat. Sci. 1384. 90 p.
- Muir, W.D., J.T. Durkin, T.C. Coley and G.T. McCabe Jr. 1984. Escape of captured Dungeness crabs from commercial crab pots in the Columbia River estuary. North Amer. J. Fish. Manage. 4: 552-555.
- Munro, J.L. 1974. The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch, and soak. J. Cons. Int. Explor. Mer. 35: 337-350.

- Noakes, D. 1986. Quantifying changes in British Columbia Dungeness crab (Cancer magister) landings using intervention analysis. Can. J. Fish. Aquat. Sci. 43: 634-639.
- Poole, R., and D.W. Gotshall. 1965. Regulations and the market crab fishery. Outdoor Calif. 26: 7-8.
- Pope, J.A., A.R. Margetts, J.M. Hamley and E.F. Akyüz. 1975. Manual of methods for fish stock assessment. Part III. Selectivity of fishing gear. FAO Fish. Tech. Paper 41 (Rev. 1) 65 p.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.
- SAS Institute Inc. 1985. SAS Institute Inc. SAS User's Guide: Statistics, Version 5 Edition. Cary N.C. 956 p.
- Schnute, J., and D. Fournier. 1980. A new approach to length frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37: 1337-1351.
- Scrivener, J.C.E. 1971. Agonistic behavior of the American lobster Homarus americanus (Milne-Edwards). Fish. Res. Board Can. Tech. Rep. 235. 128 p.
- Snow, C.D., and J.R. Neilsen. 1966. Premating and mating behavior of the Dungeness crab (Cancer magister Dana). J. Fish. Res. Board Can. 23: 1319-1323.
- Sokal, R.R., and F.J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. W.H. Freeman and Co., San Francisco. 859 p.
- Stearns, S.C. 1976. Life-history tactics: A review of the ideas. Quart. Rev. Biol. 51: 3-47.
- Stearns, S.C. 1977. The evolution of life history traits: A critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. 8: 145-171.
- Stevens, B.G., and D.A. Armstrong. 1984. Distribution, abundance, and growth of juvenile Dungeness crabs, Cancer magister, in Grays Harbor estuary, Washington. Fish. Bull. 82: 469-483.
- Thomas, D.H. 1985. A possible link between coho (silver) salmon enhancement and a decline in central California Dungeness crab abundance. Fish. Bull. 83: 682-691.
- Walters, C.J., and R. Hilborn. 1978. Ecological optimization and adaptive management. Ann. Rev. Ecol. Syst. 9: 157-188.

- Walters, C.J. 1986. Adaptive management of renewable resources. Macmillan Publishing Co. New York, New York. 374 p.
- Warner, R.W. 1985. Overview of the California Dungeness crab, Cancer magister, fisheries, p. 11-25. In B.R. Melteff [ed.] Proceedings of the symposium on Dungeness crab biology and management. Alaska Sea Grant Rep. 85-3.
- Warner, R.W. 1987. Age and growth of male Dungeness crabs, Cancer magister, in northern California. Calif. Fish and Game 73: 4-20.
- Wickham, D.E. 1979. Carcinonemertes errans and the fouling and mortality of eggs of the Dungeness crab, Cancer magister. J. Fish. Res. Board Can. 36: 1319-1324.
- Wild, P.W. 1980. Effects of seawater temperature on spawning, egg development, hatching success, and population fluctuations of the Dungeness crab, Cancer magister. Calif. Coop. Oceanic Fish. Invest. Rep. 21: 115-120.
- Williams, M.J., and B.J. Hill. 1982. Factors influencing pot catches and population estimates of the portunid crab Scylla serrata. Mar. Biol. 71: 187-192.

## PUBLICATIONS:

- Adams, N.J., and B.D. Smith. 1979. A statistical analysis of first order relationships between length and weight variables of round (fresh) and processed Atlantic herring (Clupea harengus L.). N.S. Dept. Fish. Manu. Tech. Rep. 79-01 50 p.
- Smith, B.D. 1979. Steel and plastic lobster trap trials. N.S. Dept. Fish. Manu. Tech. Rep. 79-04 37 p.
- Taylor, A.R.A., L.C-M. Chen, B.D. Smith and L.S. Staples. 1981. Chondrus holdfasts in natural populations and in culture. In: G.E. Fogg and W.E. Jones [Ed.] Proc. 8th Internat. Seaweed Symp., Bangor, Wales. p. 140-145.
- Smith, B.D., and R.E. Foreman 1984. An assessment of seaweed decomposition within a southern Strait of Georgia seaweed community. Mar. Biol. 84: 197-205.
- Smith, B.D., E.L. Cabot and R.E. Foreman. 1985. Seaweed detritus versus benthic diatoms as important food resources for two dominant subtidal gastropods. J. Exp. Mar. Biol. Ecol. 92: 143-156.
- Smith, B.D. 1985. Recovery following experimental harvesting of Laminaria longicruris and L. digitata in southwestern Nova Scotia. Helgolander Meeresunters. 39: 83-101.
- Smith, B.D. 1986. Implications of population dynamics and inter-specific competition for harvest management of the seaweed Laminaria. Mar. Ecol. Prog. Ser. 33: 7-18.
- Smith, B.D. 1988. Comparison of productivity estimates for Laminaria in Nova Scotia. Can. J. Fish. Aquat. Sci. 45: 557-562.



## **SCHOLARSHIPS AND PRIZES:**

**Province of British Columbia Postgraduate Scholarship (1986)**

**Department of Fisheries and Oceans Postgraduate Scholarship (1983-87)**

**National Research Council Postgraduate Scholarship (1976-77); declined acceptance due to a change of career plans**

**Careers '75 Province of British Columbia Research Bursary (1975)**

**Frank McLeod Whepley Undergraduate Scholarship (1973-74)**

**N. Myles Brown Undergraduate Scholarship (1973-74)**

**Canadian Association of Physicists Prize Examination; second place in the Province of New Brunswick, Saint John High School (1970)**