ASPECTS OF MULTIPAROUS SNOW CRAB (Chionoecetes opilio) FECUNDITY IN INSULAR NEWFOUNDLAND WATERS

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Aspects of multiparous snow crab (*Chionoecetes opilio*) fecundity in insular Newfoundland waters

by

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ABSTRACT

The fecundity of multiparous snow crab (*Chionoecetes opilio*) females from eight Newfoundland snow crab management areas is reported. Specimens were obtained between 1983 and 1985 when exploitation of the snow crab resource was at a very high level. Three study areas were virgin, while five were heavily fished. Basic biological data such as size (carapace width) age (shell condition) and mating status (presence of new ejaculate in the spermathecae) of each individual were collected at the time of sampling. Gravid female size ranged from 44 to 85mm carapace width (mean 65.8 mm). Fecundity was positively correlated with size ranging from 8,589 to 103,112 eggs (mean 44,658). Females from virgin areas had a higher size-specific fecundity than did those from exploited areas. Also, females utilizing new spermatophores had a higher size-specific fecundity than did those using old or a mixture of old+new spermatophores. Physical factors such as depth or latitude did not appear to affect fecundity.

The accuracy of utilizing external grasping marks as indicators of recent mating was investigated. The grasping mark status of females from three sources: nearshore time-series trapping surveys, offshore trapping and offshore trawling surveys was determined and correlated with spermathecal condition as determined by dissection. Grasping marks were found to be relatively reliable indicators of mating frequency/recency, correctly predicting spermathecal condition ~70-80% of the time. The proportion of new-shelled multiparous females that had recently mated was 1.5 times that of old-shelled multiparous females.

Fishery exploitation generally had little effect on the proportion of multiparous females bearing eggs but did have a highly significant negative impact on size-specific fecundity. Part of this effect is likely due to reduced mating frequency in exploited populations which leads to a greater reliance on stored sperm for egg fertilization.

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Finally, I wish to dedicate this thesis to my grandmother, the late Jean M. Taylor who served as a primary school teacher in rural Cape Breton Island and Newfoundland for over 30 years. She instilled in me a love of nature, taught me the difference between a root and a rhizome but made me clean my own fish.

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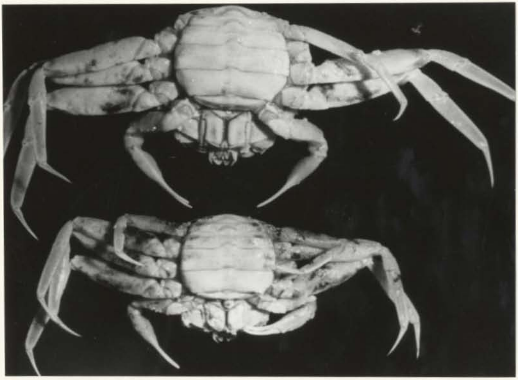

Figure 1.1A: Ventral view of mature female snow crab *Chionoecetes opilio*.

attempt to limit the snow crab harvest to within recommended exploitation rates of 50-60% (Anon. 1981) many snow crab management areas in Newfoundland have experienced harvesting levels far in excess of these guidelines (Taylor and O'Keefe 1987). It has been hypothesized that excessively high exploitation rates might negatively impact snow crab reproductive potential if many primiparous females remain unmated barren following the pubertal molt due to a lack of large males (Conan and Comeau 1986). Although recent field and laboratory studies in Newfoundland have shown that sub-legal males are capable of mating with and fertilizing multiparous females (Ennis et al. 1988, 1990), laboratory and field studies on cogener *C. bairdi* in Alaska (Paul and Paul 1996 and Stevens et al. 1993) suggest that small males have difficulty in copulating successfully with multiparous females. Therefore, the potential impact of removal of large males by commercial fisheries on the reproductive output of natural populations due to effects on individual fecundity should be evaluated.

Several snow crab management areas in NAFO Division 3L (Figure 1.2) experienced dramatic declines in landings and catch rates during the early 1980's (Taylor et al. 1994). Catch rates fell to such low levels (CPUE = kg/trap haul) between the fall of 1982 and the spring of 1983 that for all intents and purposes the fishery collapsed. In the Avalon

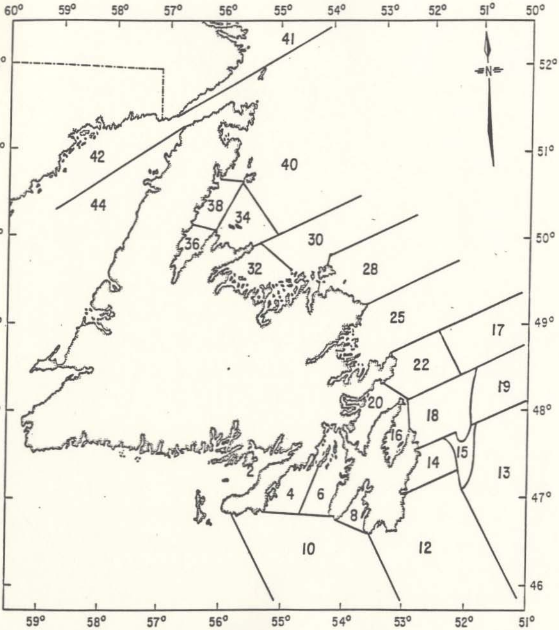

Figure 1.2: Newfoundland snow crab management areas, circa 1985.

Peninsula area (Management Areas 15, 18 and 19, Figure 1.2), fishermen virtually abandoned the fishing grounds between 1985 and 1988 due to the scarcity of commercially acceptable male snow crab (Taylor et al. 1994). This situation presented an opportunity to examine the reproductive status of mature females to determine whether the decline in large males for a period of several years had impacted either the proportion of mature females that carried eggs or the number of eggs females carried.

Reproductive Biology

Most researchers believe that female *C. opilio* and their congeners undergo a terminal molt to maturity in the winter or early spring when they are between 5-7 years old (Yoshida 1941; Ito 1963; Watson 1970, 1972; Hilsinger 1976). This molt to maturity usually takes place with the assistance of a male partner while in the pre-copulatory embrace (Watson 1970, 1972; Hooper 1986; Donaldson and Adams 1989; Sainte-Marie and Hazel 1992). However, Ito and Kobayashi (1967) and Hooper (1986) have reported mature females (identified by the presence of a wide rounded abdomen) in the process of molting. Following copulation, females extrude bright orange eggs for the first time, and are termed "primiparous". Females that repeat spawn a second or third time in later years are referred to as "multiparous". The eggs are attached to pleopods (Figure 1.3) that are present on the underside of the abdominal flap. The eggs become progressively darker during the incubation period as the eyespot enlarges during development. The eggs undergo an incubation period ranging from one year (Watson 1972) to slightly more than two years (Sainte-Marie 1993) before pre-zoeal stages are released in the spring immediately prior to, or just after re-mating (Taylor et al. 1985; Hooper 1986).

Various aspects of female *Chionoecetes* sp. fecundity have been studied in recent years. These studies and their findings are briefly summarized in Table 2.1. Sperm storage and the functional anatomy of the female *C. opilio* spermathecae have been studied by several researchers (Beninger et al. 1988; Sainte-Marie 1993; Sainte-Marie and Lovrich 1994). Mating behaviour of *C. opilio* based on laboratory observations has been described by Watson (1972) while field studies have been carried out by Taylor et al. (1985), Hooper (1986), Ennis et al. (1988, 1990) and Comeau et al. (1993).

The primary objective of the present study is to investigate the impact of the commercial fishery on female snow crab reproductive biology in the waters surrounding insular Newfoundland. Previous comparisons of the proportion of mature females carrying eggs have revealed

Figure 1.3: Clutch of orange eggs attached to the pleopods of a mature female snow crab.

Table 2.1. Relation of fecundity (Y, # eggs) to carapace width (X, mm) for snow crab *Chionoecetes opilio* from several study areas.

Study Area	Sample size	Fecundity regression	$\bar{x}$ fecundity (# of eggs)	Range
Newfoundland[a]	51	$Y = 6.4080X^{2.169}$	52,048	37,934 - 81,239
Newfoundland[b]	350	$Y = 0.7493X^{2.6108}$	44,658	8,589 - 103,112
Baie Sainte-Marguerite[c]	195	$Y = 0.7311X^{2.725}$	45,273	17,181 - 109,757
Anticosti[a]	98	$Y = 13.2530X^{1.9922}$	58,760	12,134 - 122,891
Pleasant Bay[a]	98	$Y = 38.4554X^{1.7649}$	74,475	32,564 - 128,433
Gabarus[a]	115	$Y = 14.7361X^{1.9859}$	80,068	42,284 - 120,378
Gulf of St. Lawrence[e]	99	$Y = 0.0012X^{4.200}$	-	20,000 - 140,000
NW Cape Breton Island[d]	25	$Y = 3092.23X^{0.70}$	61,430	31,276 - 102,022
Southeastern Bering Sea[e]	42	$Y = 0.4905X^{2.7206}$	36,273	-- -

[a] from Davidson (1983)
[b] from present study
[c] from Sainte-Marie (1993)
[d] from Elner and Gass (1984)
[e] from Haynes et al. (1976)

little difference between regions that had varying levels of exploitation (Elner and Gass 1984). Data presented herein for the Newfoundland region are similar with the possible exception of periods when molting rates decline severely. Potential effects on individual fecundity have not been previously investigated. In the present study, fecundity is compared among several areas experiencing varying degrees of commercial exploitation revealing highly significant differences between exploited and virgin stocks. Differences among sites were also examined for trends relative to physical features such as depth and latitude. These differences were further examined to determine the relative effects of male size, age as indicated by female shell condition and recency of mating as indicated by spermatophore type. This analysis reveals a strong spermatophore affect indicating that mating recency significantly affects size-specific fecundity.

Finally, the efficacy of determining recency of mating from external observations of grasping marks is evaluated by comparison with internal spermathecal observations. This is a potential tool for rapid evaluation of the mating status of commercially exploited populations.

CHAPTER 2: Snow Crab Fecundity

INTRODUCTION

One of the principal methods used to ascertain the reproductive "health" of snow crab populations has been the monitoring of the proportion of mature females carrying eggs. If an exploited population is undergoing stress in terms of fulfilling its reproductive potential this could manifest itself as an increase of barren females. If barren females are extremely old-shelled then they could be classified as being reproductively "senile" (Elner and Beninger 1995). This should be considered a normal part of the life cycle and the numbers of such females in a population at a given time would be dependent on recruitment strength, natural mortality and possible discard mortality. However, if a high percentage of barren females in an exploited population are relatively young, then it is possible that the removal of large males might have a negative impact on population fecundity. High percentages of barren females have been observed off Cape Breton Island (Elner and Robichaud 1986) and the Nearshore Avalon Peninsula area (Taylor and O'Keefe 1986).

While development of an index of the percentage of females carrying full clutches of eggs may provide an overview of the population reproductive "health" in relation to exploitation rates and recruitment fluctuations, individual size-specific fecundity can be used to assess and individual fitness in terms of egg number or mass (Elner and Beninger 1995).

METHODS

Time-series research cruises were carried out each year from 1982-92 in three heavily exploited nearshore areas; Bonavista Bay, Conception Bay and Nearshore Avalon. Specimens were obtained by baited traps and females were separated from males and sampled separately. Maturity, carapace width, shell condition and size and developmental stage of the egg clutch were recorded for each individual female.

Size-Specific Fecundity

Specimens from some of these yearly, nearshore cruises and from opportunistic spring offshore cruises were examined to determine the reproductive status of females. A number of locations from areas with different exploitation rates and bathometric features were chosen in an attempt to obtain samples from as diverse a range of areas as possible. Samples were collected from the following snow crab management areas:

Virgin Areas

Much of the data collection for this study was conducted during a period of extensive areal fishery expansion as the crab fleet sought new fishing grounds to replace those where catch rates had fallen to unacceptably low levels. Two areas on the east coast of insular Newfoundland, Fogo Island and the Downing Basin, were identified as virgin grounds and samples were obtained shortly after fishing activity was initiated. Fishing had always been prohibited in a third area, Bonne Bay, on the west coast of the Island until 1985 when an illegal fishery had decimated the standing stock of mature crabs (Ennis et al. 1990). The information available indicates that this stock had never been previously fished. Specimens collected from this area were obtained prior to the inception of the illegal fishery.

The virgin areas can be described as follows:

Bonne Bay [Figure 2.1 (a)]: This area situated on the west coast of the Island of Newfoundland is a fjord in which there is a virgin population of snow crab that has been studied extensively (Taylor et al. 1985), Hooper 1986, Ennis et al. 1988, 1990 and Comeau et al. 1994). Although commercial fishing only began in this management area (Area 44, Figure 1.2) in 1995,

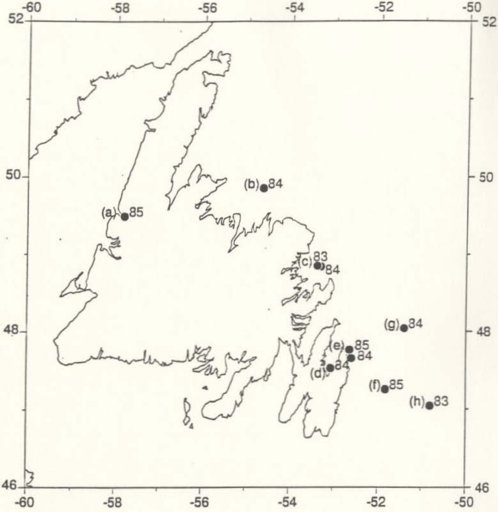

Figure 2.1: Sample sites where mature multiparous females were collected for fecundity analysis: a) Bonne Bay, b) Fogo Island, c) Bonavista Bay, d) Conception Bay, e) Nearshore Avalon, f) Southern avalon, g) Offshore Avalon and h) Downing Basin.

anecdotal evidence indicates that in the late fall of 1985 illegal fishing activity severely depleted the resource.

Fogo Island [Figure 2.1 (b)]: This area is located on the northeast coast of the island and was first fished in 1984. The commercial crab fishing grounds are comprised of many isolated deep holes. While the area has been heavily exploited since it was first fished, specimens examined herein were collected during the early summer of 1984 and are thus considered as coming from a virgin area.

Downing Basin [Figure 2.1 (h)]: This area was first fished (at a low level of effort) in 1981, approximately 9 months before the date samples were collected. For the purposes of this study, females collected during the spring of 1982 are considered as having come from virgin grounds. This area was rapidly fished out in 1982-83 and subsequently was virtually abandoned by the commercial crab fleet due to the long distance from shore and extremely low catch rates.

Exploited Areas

Many areas along the northeast coast of Newfoundland have been fished since the early 1970's. Within this group of exploited areas there is wide variability in terms of exploitation rates and bottom substrate type. The commercially exploited areas selected for this study effectively represent the various types of fishing grounds prevalent at this time. The exploited areas from which samples for this study were collected are described as follows:

Bonavista Bay [Figure 2.1 (c)]: The snow crab resource in this area has been subject to very heavy fishing pressure since the late 1970's. The commercial fishing grounds are located in a deep trough that runs more or less continuously from the head to the mouth of the bay.

Conception Bay [Figure 2.1 (d)]: This area has been periodically subjected to extremely heavy fishing pressure and despite remedial action in terms of markedly reduced quotas, CPUE recovery has been slow (Taylor and O'Keefe 1988). The fishing grounds in this area are restricted to a deep-water trough that runs through the centre of the bay.

__Nearshore Avalon__ [Figure 2.1 (e)]: In the early 1980's the snow crab resource in this area was so severely depleted that commercial activity virtually ceased (Taylor et al. 1994). This period of reduced abundance lasted from 1982 until 1988. The commercial fishing grounds are generally restricted to depths in excess of 185 m and are more or less continuous. A reduction in the percentage of berried females was detected in 1985 (Taylor and O'Keefe 1986), providing the stimulus for the present study.

__Southern Avalon__ [Figure 2.1 (f)]: The fishery in this area at the time specimens were collected was centered on commercial grounds that were quite restricted in area and therefore subject to intensive fishing activity and high exploitation rates.

__Offshore Avalon__ [Figure 2.1 (g)]: This area, which was first exploited in 1981, experienced a collapse in resource abundance in the mid 1980's following the transfer of effort from the Nearshore Avalon. The commercial fishing grounds in this area consist of a series of three large "holes" progressively farther offshore that were all fished during the first year of commercial exploitation.

Specimen Collection - Fecundity Analysis

This aspect of the study examined the reproductive status of 350 mature berried females from several snow crab management areas around insular Newfoundland between 1983 and 1985. Only females bearing full clutches of bright orange eggs were retained for fecundity studies. Specimens were collected using standard Japanese-style conical crab traps baited with a mixture of northern short-finned squid (*Illex illecebrosus*) and Atlantic mackerel (*Scomber scombrus*). Traps were fished in randomly selected positions stratified by depth in longline fleets of 12. Weather permitting, fishing gear was hauled after a 24 h soak. Eleven traps were fitted with standard commercial crab mesh (133 mm stretch measure) and one trap per fleet was covered with small-meshed (25 mm stretch measure) webbing to obtain a sample of sub-legal sized crabs (including females) that normally escape through commercial mesh.

Upon hauling the traps, crabs were sorted according to sex. If the number of female snow crabs exceeded 25-30 individuals, then the catch was subsampled into two baskets. Female crabs in one basket were counted and returned to the sea immediately; those in the other basket were retained as a representative biological sample. Samples were collected between April and July except for the Bonne Bay and Conception Bay samples which were collected in October.

Since sampling was conducted opportunistically during surveys directed primarily at male crabs, females were collected as they were encountered. In some areas all or most of the females used in this study were collected from one or two locations. In most areas however, they were collected in small batches or individually. Biological sampling entailed measuring the carapace width (CW) to the nearest 1.0 mm at its widest point, and classifying the molt stage as determined by shell condition according to the following criteria (Taylor et al. 1989):

1. **"New-soft"** - recently molted crabs having an extremely soft shell bearing no epibiotic growth.

2. **"New-hard"** - hard-shelled crabs having very little epibiotic growth on their shells. Crabs in this shell condition could be either primiparous or multiparous.

3. **"Old-hard"** - hard-shelled crabs carrying large amounts of epibiotic growth on their carapaces. Crabs in this shell category are considered multiparous.

Evidence of the recency of mating was collected by dissecting the animal and macroscopically determining whether the spermathecae contained old or new spermataphores or both (see Chapter 3). A representative size range of females carrying full broods of orange eggs was chosen randomly for fecundity studies. Egg masses were removed intact with the pleopods by severing the abdomen from the body, and then fixing the mass in 10% formalin buffered with sea water.

Egg Counts and Mass

Fixed egg samples were drained, rinsed with distilled water and soaked in Gilson's fluid for 24 hours. Eggs were then stripped from the pleopods with fine forceps, carefully pressed through a 800 mm sieve in order to separate them from each other and captured on a 355 mm sieve. Each egg sample was placed in a pre-weighed aluminum boat, oven dried for 24 h at 65°C and then total egg mass was determined to the nearest 0.1 mg. The total number of eggs for each clutch was estimated from counts of two small subsamples weighing approximately 40 mg and containing 500-700 eggs.

Statistical Analysis

The general allometric relationship between fecundity, measured in terms of egg number or total egg mass, and female size (measured as carapace width) was determined by log:log regression. The additional effects of category variables such as fishery status (virgin vs. exploited) capture location, spermatophere type (new vs. old), and female age (new vs. old shell) were investigated by analysis of covariance using dummy variables in a multiple regression model (Nie 1975). Each variable was coded as a binary dummy variable, i.e. "1" if a virgin area and "0" if an exploited area, and then was tested in a multiple regression already containing log carapace width to see if it explained additional significant variation in the elevation of the line (the intercept). The resultant model was of the general form:

$$\log F = A + B_1 D_1 + B_2 D_2 \;\ldots.\; + B_N \log CW$$

where F is the fecundity, CW is carapace width, A is the intercept, B_i are the regression coefficients and D_i are the dummy variables such as fishery status, sperm type, etc. This model formulation has the advantage that the effect strengths of the category variables may be readily calculated by converting back to linear form. For example, the linear form of a model with only one dummy variable (D_1) representing fishery status (virgin = 1, exploited = 0) would be:

$$F = 10^{A} * 10^{B_1 D_1} * CW^{B_2}$$

For an exploited area, $10^{B_1 D_1}$ returns a value of 1 which has no effect on calculated fecundity (i.e. it is the reference group) while for a virgin area $10^{B_1 D_1}$ has the value of 10^{B_1} . If the regression coefficient B_1 had a value of 0.0615 then the effect strength of the dummy variable "Virgin" would be $10^{0.0615} = 1.152$. This would indicate that the size-specific fecundity of females from virgin areas was on average 1.152 times that of females from exploited areas; in other words, 15.2% greater. Histograms and normal probability plots of the standardized residuals were examined at each step of model construction to check for departures from normality.

RESULTS AND DISCUSSION

Fecundity was examined on two levels. Firstly, the percentage of females carrying eggs from time-series research cruises conducted in three heavily exploited commercial fishing areas was examined on a yearly basis from 1982-92. Secondly, the individual fecundity in terms of egg numbers and egg mass of selected females was assessed for a number of areas with varying physical and biological factors and supporting varying levels of commercial exploitation.

Percentage of Ovigerous Females

A summary of the percentage of berried (egg-carrying) females for three commercial fishing areas from 1982-92 is presented in Table 2.2. With the exception of Nearshore Avalon in 1982 and 1983, when sample sizes were very low, the percentage of berried females ranged between 81-100% and usually exceeded 90%. There was an apparent decline in the percentage of berried females detected during annual spring research cruises in the Nearshore Avalon area between 1985 and 1987. The significance of this decline has been briefly discussed in Taylor and O'Keefe (1986) who noted that virtually all molting activity was curtailed during this period, possibly due to lower than usual water temperature (<-1.3°C). This cessation of molting activity precipitated a fishery collapse since no males recruited into the fishery for a number of years (Taylor et al. 1994). In contrast, the percentage of berried females in Bonavista Bay (an extremely heavily exploited area) remained relatively stable and above the 90% level. Although molting activity in this bay was somewhat reduced during this time it was still at a comparatively high level (Taylor et al. 1994) as evidenced by the comparatively high initial catch rates experienced by the commercial fleet each year and by the high proportion of new-shelled legal-sized males captured during annual

Table 2.2: Summary of the percentage of mature females bearing eggs on the commercial fishing grounds of 3 snow crab, *Chionoecetes opilio*, management areas 1982-92.

YEAR	BONAVISTA BAY	CONCEPTION BAY	NEARSHORE AVALON
1982	100 (N=86)	100 (N=74)	72.7 (N=22)
1983	100 (N=1395)	-	33.3 (N=6)
1984	97.8 (N=1008)	98.2 (N=110)	98.8 (N=172)
1985	97.5 (N=400)	98.5 (N=522)	94.4 (N=36)
1986	96.0 (N=298)	100 (N=166)	92.3 (N=1716)
1987	99.0 (N=394)	96.8 (N=758)	85.7 (N=224)
1988	100 (N=286)	92.3 (N=1090)	92.9 (N=480)
1989	94.9 (N=472)	80.8 (N=396)	90.0 (N=240)
1990	99.7 (N=580)	-	97.9 (N=762)
1991	97.9 (N=676)	98.1 (N=318)	99.2 (N=524)
1992	100 (N=378)	100 (N=30)	100 (N=182)

research cruises (Taylor and O'Keefe 1986). Thus it seems that the effect of exploitation on the proportion of berried females is relatively weak except when accompanied by extreme environmental conditions.

Individual Fecundity

The reduction in the abundance of commercial-sized and presumably sexually competent male snow crab provided an opportunity to determine whether the decline in abundance of large males in a population affected the fecundity and general "reproductive health" of females on an individual basis.

Size-Specific Fecundity

Egg mass and number were determined for 350 female snow crabs from 8 management areas. Females ranged in size from 44-85 mm carapace width with a mean width of 65.8 mm. Fecundity, in terms of the number of eggs attached to the pleopods, ranged from 8,589 to 103,112 while overall mean fecundity irrespective of area was 44,658 eggs (Table 2.1). In all study areas combined, individual fecundity was positively correlated with size, increasing exponentially with increasing carapace width (Figure 2.2). No between-year statistical differences were observed (ANOVA, $p > 0.05$) in the mean fecundity of females from Bonavista

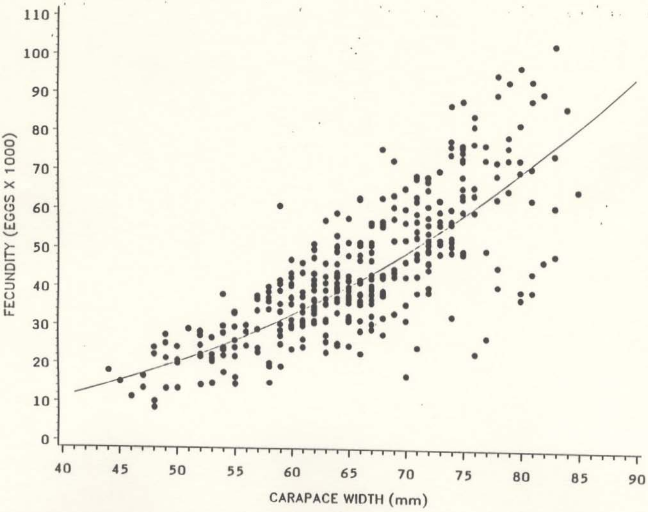

Figure 2.2: Scatter plot and regression of fecundity (egg number) versus carapace width for females from all study areas combined

Bay and nearshore Avalon Peninsula management areas therefore data for all years from these areas were combined for further analyses.

Virgin Versus Exploited Areas

Analysis of covariance using multiple linear regression (see example in methods) analysis indicates that females from the three virgin management areas (Bonne Bay, Downing Basin and Fogo Island) were 15.2% more fecund in terms of egg numbers/clutch than were same-sized females in commercially exploited areas (Table 2.3). Females from Fogo Island, demonstrated a smaller size-specific fecundity effect than those from the other virgin areas. This result may be attributable to the prior fishing history in that the commercial crab-fishing grounds had historically supported a heavy groundfish gillnet fishery with reported high levels of (large male) snow crab by-catch (Miller and Hoyles 1973). The gillnet fishery for groundfish may have acted in a similar manner as a directed fishery in reducing the number of large males available for mating.

Fecundity in terms of total mass of the egg clutch was also examined in order to minimize variability associated with within-clutch differences in egg size and intra/inter area variability of egg size (Davidson et al. 1985; Sainte-Marie 1993). Regression analysis of egg clutch mass

Table 2.3: Summary of size-specific fecundity effects on snow crab egg numbers and egg mass by sample area and fishery exploitation status. (V) denotes virgin areas

			CARAPACE WIDTH vs EGG NUMBER				CARAPACE WIDTH vs EGG MASS			
CATEGORY VARIABLE	n	$\bar{x}$ male size (CW mm)	t value	signif.	coeff.	effect	t value	signif.	coeff.	effect
VIRGIN vs EXPLOITED			5.15	<.0001	.0615	+15.2%	7.38	<.0001	.09366	+24.1%
CAPTURE LOCATION										
FOGO ISLAND (V)	37	105	0.48	.6281	.01091	+ 2.5%	0.28	.7776	.0069	+ 1.6%
BONAVISTA BAY	79	98	1.42	.1561	.02027	+ 4.8%	-0.74	.4577	-.01152	- 2.6%
CONCEPTION BAY	37	91	-1.96	.0514	-.03778	- 8.3%	-2.40	.0167	-.05025	-10.9%
NEARSHORE AVALON	56	94	-3.20	.0015	-.05168	-11.2%	-2.38	.0180	-.04188	- 9.2%
OFFSHORE AVALON	16	104	-1.65	.0990	-.0473	-10.3%	-1.88	.0616	-.05806	-12.5%
DOWNING BASIN(V)	44	103	4.56	<.0001	.08116	+20.5%	7.23	<.0001	.13386	+36.1%
SOUTHERN AVALON	33	N/A	-3.13	.0019	-.06343	-13.6%	-3.57	.0004	-.07807	-16.5%
BONNE BAY (V)	48	116	2.52	.0121	.04541	+11.0%	3.20	.0015	.06209	+15.4%

against carapace width revealed that the three virgin areas again had a higher size-specific fecundity for each size group than did commercially fished areas. In fact, fecundity in terms of egg mass was 24.1% higher in virgin than in exploited areas. This difference in range between fecundity levels measured as egg numbers versus egg mass implies that egg size is correlated with egg mass. The observed correlation between egg mass and egg size, calculated as egg mass/egg number, was indeed highly significant ($r = -.463$, $p < .0001$). This indicates that large egg masses generally contained smaller eggs.

The magnitude of fecundity effects varied widely among areas ranging from -13.6% for the commercially exploited Southern Avalon area to +20.5% for the virgin Downing Basin area (Table 2.3, Figure 2.3). In terms of egg mass as a measure of fecundity the effects ranged from -16.5 for the Southern Avalon to +36.1% for the Downing Basin. This wide range of variation provides an opportunity to explore the effects of physical variables (latitude and depth) and biological variables (male size, shell condition and spermatophore type) on size-specific fecundity.

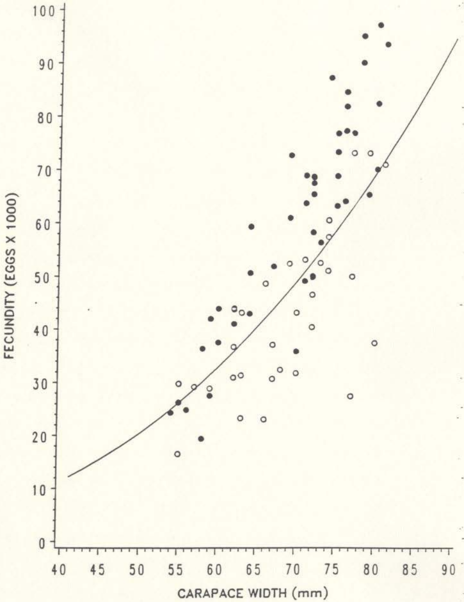

Figure 2.3: Scatter plot and regression of fecundity (egg number) versus carapace width for females from Downing Basin (solid figures) and Southern Avalon (open figures).

Physical Variables

Latitude

Jones and Simms (1983) demonstrated that latitudinal differences can influence fecundity in the mud crab *Helice crassa* in New Zealand. Fecundity, measured over a range of approximately 11.5 degrees latitude, was highest in terms of egg number at the highest latitude, total egg mass was independent of latitude. There were no obvious latitudinal trends in the present data for Newfoundland snow crab (Table 2.4, Figure 2.4). However, effects could possibly be obscured by differences in the exploitation level of the areas surveyed. Examination of the virgin areas alone reveals a negative trend with latitude, contrary to expectation. Downing Basin had the highest fecundity effect in terms of both egg mass and egg numbers whereas the two northerly sites (Fogo Island and Bonne Bay) had lower fecundity (Figure 2.4). Latitudinal range (~3 degrees) sampled in this study was narrower than that of the New Zealand study and latitude effects could also be obscured by other sources of variation. It should be noted that although these results are contrary to the expected trend, only three virgin sites are represented.

Table 2.4: List of fecundity sample sites with navigational coordinates.

SAMPLE LOCATION	LATITUDE	LONGITUDE
FOGO ISLAND	49 55.6′	54 14.0′
BONNE BAY	49 33.1′	57 54.7′
BONAVISTA BAY	48 50.8′	53 22.5′
OFFSHORE AVALON	48 02.5′	51 24.9′
NEARSHORE AVALON	47 46.5′	52 11.7′
CONCEPTION BAY	47 23.2′	52 56.8′
SOUTHERN AVALON	N/A	N/A
DOWNING BASIN	47 02.3′	50 48.3′

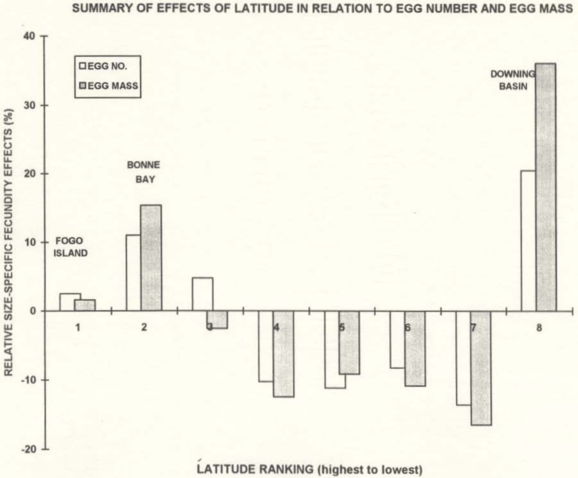

Figure 2.4: Size-specific fecundity versus latitude.

Depth

Although temperature has been observed to affect egg development time (Mallet et al. 1993) fecundity effects have not been reported. There are no seasonal temperature data for the collection areas reported herein but it is expected that temperature should vary inversely with sampling depth which (except for the Southern Avalon area) was recorded.

Mean depths of the areas sampled exhibited no obvious correlation with the fecundity differences observed among areas (Figure 2.5). The two areas with highest fecundity, Downing Basin and Bonne Bay, had mean depths that bracketed that of two of the lowest fecundity areas (Offshore Avalon and Nearshore Avalon).

The fact that fecundity does not appear to be related to depth does not rule out the possibility of such an effect because the depth at which females were caught may not be representative of their average depth at the time that they were incubating eggs. Studies of long-term movements of male snow crab (Watson and Wells 1972; Taylor 1992) demonstrate that crabs can move more than 15 km over a one year period. Other studies have documented seasonal changes in depth distribution for males (Miller and O'Keefe 1981) as well as for both sexes (Lovrich et al. 1995). Sainte-Marie and Hazel (1992) also describe molting of immature male and female snow crab in shallow waters of the northwestern Gulf

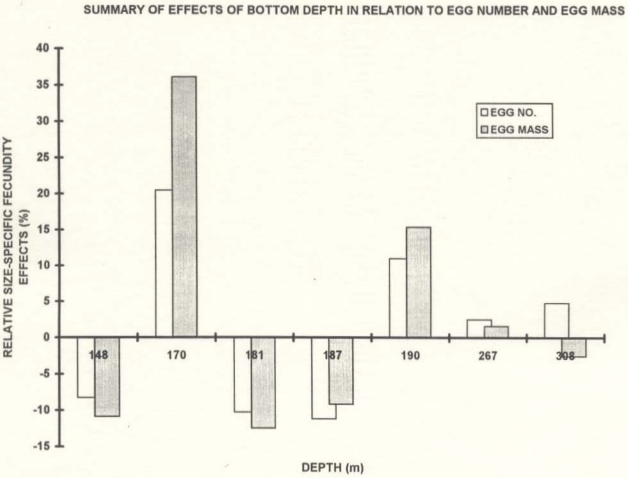

Figure 2.5: Size-specific fecundity versus depth.

of St. Lawrence. Lovrich et al. (1995) document mature and immature males and females moving to comparatively shallow water in the winter and moving progressively deeper during spring and summer. The mating migration from deep to shallow water in the early spring has also been well-documented in Bonne Bay (Taylor et al. 1985; Hooper 1986; Ennis et al. 1988, 1990; Comeau et al. 1991).

Biological Data

Male Size

The mean size of males captured coincidentally with the females (Table 2.3) showed no apparent trend with relative fecundity (Figure 2.6). Bonne Bay males were much larger on average than those from other areas (mean CW 116 mm), while those from Conception Bay and the Nearshore Avalon were much smaller. However, there was very little difference in the mean size of males from the other areas which displayed a wide range of fecundity effects from the highest (Downing Basin), to among the lowest (Offshore Avalon) (Figure 2.6). Thus, there was no obvious correlation between fecundity and the size of simultaneously captured males. The fact that no pattern was observed in these field data should again not be taken as evidence against the potential existence of male size effects because the actual size of successfully mating males was unknown. It has been reported that large males

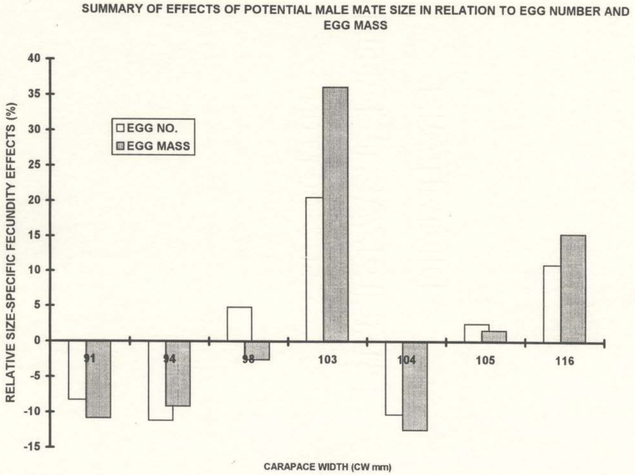

Figure 2.6: Size-specific fecundity versus mean size of concomitantly captured male snow crab.

have a higher rate of mating success than small males (Hooper 1986; Conan and Comeau 1986) although actual effects of male size on size-specific fecundity have yet to be documented.

Shell Condition - Age Effects

Older multiparous females, as determined by shell condition (old-hard, see methods) had significantly lower fecundity than younger (new-hard) multiparous individuals (Table 2.5). Females with new shells were 10.5% and 9.0% more fecund than old-shelled individuals in terms of egg numbers and egg mass respectively.

Previouisly, researchers (Haynes et al. 1976; Jewett 1981; Elner and Robichaud 1983) speculated that primiparous females might have a lower fecundity than multiparous female *C. opilio*. This was recently confirmed by Sainte-Marie (1993) for specimens collected in the northern Gulf of St. Lawrence. He demonstrated that primiparous females were 16.4-22.7% less fecund that young multiparous females of the same size. These observations, combined with the age effect observed here, indicate that population age structure can have significant effects on overall fecundity of snow crab populations. Populations dominated by either young primiparous or old multiparous females should have lower

	CARAPACE WIDTH vs EGG NUMBER				CARAPACE WIDTH vs EGG MASS			
SHELL TYPE	t value	signif.	coeff.	effect	t value	signif.	coeff.	effect
NEW HARD vs OLD HARD	2.241	0.0257	.04338	+10.5%	1.777	.0764	.03740	+9.0%

Table 2.5. Comparison of size-specific effects of shell type on fecundity.

fecundities than those with a more balanced age distribution.

Spermatophore Type

Covariance analysis conducted on 253 individuals by spermathecal contents indicates that females carrying new spermatophores had higher fecundity than those with old spermatophores while females with both old and new spermatophores were intermediate (Table 2.6). Females with either new spermatophores or new + old spermatophores were both significantly more fecund in terms of egg numbers than those with old spermatophores only. The analysis of fecundity in terms of egg mass revealed a significant difference between new and old spermatophores only. The size-specific fecundity difference between old and new spermatophores was 30.3% for egg number and 21.0% for egg mass (Table 2.6). The observation that size-specific fecundity tended to be higher in females with new spermatophores than in those with both new + old spermatophores (although not significantly so: $p = 0.11$ for eggs, 0.18 for egg mass) was unexpected because new spermatophores are at the base of the spermathecae and thus should be utilized first during fertilization.

Table 2.6: Pairwise comparison of spermatophore type effects on size-specific fecundity in terms of egg number (upper right section) and egg mass (lower left section). Each cell contains the effect coefficient followed by its p value, sample size and calculated effect strength.

	NEW	NEW + OLD	OLD
NEW		0.05151 p=0.1060 N=130 +12.6%	0.11478 p<0.0001 N=140 +30.3%
NEW + OLD	-0.04422 p=0.1787 N=130 -10.7%		0.02945 p=0.0402 N=236 +7.0%
OLD	-0.10231 p=0.0002 N=140 -21.0%	-0.02612 p=0.0813 N=236 -5.8%	

Joint Analysis of Shell Type and Spermatophore Type Effects

A stepwise model of the joint influence of spermatophore type and shell condition revealed that shell condition did not explain significant additional variance in size-specific fecundity when added to models containing spermatophore effects (models 1 and 3 in Table 2.7). In contrast, spermatophore type explained significant additional variation in size-specific fecundity measured as egg number when added to a model that already contained shell condition (model 2 in Table 2.7) while the extra explained variance for predicting egg mass was at the borderline of significance (model 4 in Table 2.7). Therefore the shell condition effect seems to be weaker than the spermatophore effect. The two factors are partly confounded statistically because new-shelled females tend to have new spermatophores ($r = 0.523$).

The "virgin area" factor contained significant independent information additional to each of the above models (see "remaining variables" in models 1-4, Table 2.7). This indicates that there are explanatory factors other than spermatophore type and shell condition that remain to be elucidated.

Table 2.7: Stepwise regression models of fecundity versus carapace width and biological and site factors.

Dependent Variable : Log Egg Number

MODEL 1				
Independent Variables	β	r^2	t	p
New Ejaculate	-0.0688	0.651	2.37	0.0184
Old Ejaculate	-0.0291	0.657	-2.06	0.0404
Constant	-0.0975		-0.44	0.6607
Remaining Variables				
New Shell			0.96	0.3355
Virgin Area			2.88	0.0044
MODEL 2				
Independent Variables	β	r^2	t	p
Log Carapace Width	2.5994	0.638	20.75	<0.0001
New Shell	0.0407	0.647	1.92	0.0563
Old Sperm	-0.0313	0.654	-2.22	0.0275
Constant	-0.1088		-0.48	0.6348
Remaining Variables				
New Ejaculate			1.69	0.0922
Virgin Area			3.09	0.0022

Table 2.7: (Continued)

Dependent Variables: Log Egg Mass

MODEL 3				
Independent Variables	β	r^2	t	p
Log Carapace Width	2.8211	0.661	22.36	<0.0001
New Ejaculate	0.0748	0.670	2.57	0.0105
Constant	-0.7176		-3.13	0.0019
Remaining Variables				
Old Ejaculate			-1.75	0.0811
New Shell			0.86	0.3919
Virgin Area			3.35	0.0009
MODEL 4				
Independent Variables	β	r^2	t	p
Log Carapace Width	2.8256	0.661	21.78	<0.0001
New Shell	0.0427	0.667	1.99	0.0470
Constant	-0.7268			
Remaining Variables				
New Ejaculate			1.83	0.0683
Old Ejaculate			-1.93	0.0544
Virgin Area			3.58	0.0004

SUMMARY

The results of the investigation into snow crab fecundity can be summarized as follows:

1. The observed percentage of berried females in snow crab populations usually was high (>90%) and was largely independent of the commercial exploitation rate.

2. Size-specific fecundity of females in virgin areas was higher than that of those in commercially exploited areas. A significant portion of this higher fecundity can be attributed to spermatophore type with females possessing new spermatophores significantly more fecund in terms of both egg number and egg mass. From this it can be inferred that recency of mating affects fecundity, i.e. multiparous females utilizing new spermatophores are more fecund than those relying on old spermatophores from a previous mating.

3. The enhanced fecundity bestowed by new spermatophores suggests that a rapid method of assessing recency of mating might be useful in comparing snow crab population reproductive status.

CHAPTER 3: External Classification of Mating Recency

INTRODUCTION

The analysis of size-specific fecundity has revealed a strong effect related to spermatophore type (Chapter 2). Females bearing only old sperm had significantly lower fecundity than those bearing new spermatophores. This suggests that recency of mating should be correlated with individual fecundity and thus might be used as an indicator of population reproductive status.

One way the male only commercial snow crab fishery might thus affect reproductive output of a population would be through reduced frequency of mating possibly due to either reduced male density and/or size. There is strong competition among males both for primiparous (Sainte-Marie and Hazel 1992) and multiparous (Hooper 1986; Conan et al. 1994) females. Larger snow crab males have been observed in the laboratory (Conan and Comeau 1986) and in situ (Hooper 1986) to be more effective than smaller males in securing and mating females. Some of the implications of depletion of large males have been discussed by Sainte-Marie and Lovrich (1994), Conan and Comeau (1992), Elner and Beninger (1995) and Ennis et al. (1990). Heavy fishery exploitation will shift the population from a relatively static state comprised for the most part of large, old-shelled morphometrically mature male and multiparous females to a population dominated by new-shelled smaller individuals (Ennis et al. 1990; Conan et al. 1992). These expected changes in size distribution can be observed in Newfoundland snow crab populations. For example, the virgin population in Bonne Bay was dominated by large old-shelled males (Figure 3.1) while heavily exploited populations such as that in Conception Bay had much smaller males with a smaller size range (Figure 3.1) (see other concomitant male size frequency distributions in Appendix 1).

Such large changes in male size distribution might affect the frequency of mating by females. This would in turn affect the proportion of multiparous females bearing new spermatophores which has been shown to affect fecundity (Chapter 2). It would thus seem valuable to have a rapid means of assessing mating recency in natural populations so that potential fishery exploitation effects could be monitored. Frequency of mating could be determined for multiparous females by measuring the proportion carrying new spermatophores but this requires sacrificing the animals for internal examination which is often difficult to do under field operating conditions and can in any case be time-consuming. Therefore, it would be useful if a more expedient and less destructive indicator of mating recency were available. Grasping marks left by males on hard-shelled multiparous females might be such an indicator.

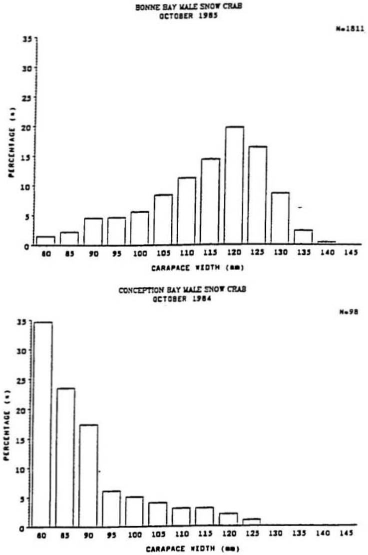

Figure 3.1: Comparison of size-frequency distribution of concomitantly capture male snow crabs from a virgin area (Bonne Bay) and a heavily exploited area (Conception Bay).

During the precopulatory and copulatory mating embrace, the male holds onto and immobilizes its mate by grabbing her periopods with his chelae (Watson 1972; Taylor et al. 1985; Hooper 1986). Primiparous females mate in the soft-shelled condition and their pliant exoskeleton does not usually bear grasping marks (Paul 1984), thus making it extremely difficult to observe any external indicator of mating unless they are examined within a matter of days. In contrast, the mating embrace causes abrasions and scaring of the shell of hard-shelled multiparous females which leave detectable grasping marks. As the shell of the female ages, so do the grasping marks it bears. Grasping marks which are initially bright-light coloured abrasions become dull and discoloured over time. Frequently they become infected by chitonoclastic bacteria which cause a slight necrosis of the shell tissue, turning the scars black.

Grasping marks have previously been used to assess the recency of the mating embrace during the annual mating migration in Bonne Bay (Taylor et al. 1985; Hooper 1986) and also in laboratory pairing experiments to evaluate the mating capability of small males (Ennis et al. 1988). The efficacy of using grasping marks as an indicator of mating success for females captured on the commercial fishing grounds is herein evaluated by comparing external observations of grasping marks with internal examination of spermathecal contents.

METHODS

During the period 1987-92 inclusive, time-series cruises were conducted off the northeast portion of the Avalon Peninsula (Figure 1.2, Management Area 18). These cruises were carried out in the spring, when mature females would be best suited for testing whether the presence of fresh grasping marks provided a reliable indicator of recent mating. Mating status was determined by qualitative internal observations of the condition of the paired spermathecae to determine the age of spermataphores, and by qualitative external observations on the grasping marks on the walking legs.

Spermathecae Observations

Macroscopic observations of the spermathecae were accomplished by simply removing the carapace and teasing out the spermathecae from the visceral mass. Spermathecae were classified into the following categories defined by the colour and texture of the spermathecal contents (Adams and Paul 1983; Paul 1984):

1. **NEW ONLY** - Spermathecae having a very full appearance and containing only a bright-white, semi-solid matrix of spermataphores "capped" by a thin layer of brown gel (Figure 3.2).

2. **OLD & NEW** - Spermathecae consisting of two distinct layers of ejaculate. The apical portion of the spermathecae containing a hard, yellowish to cream-coloured ejaculate "capped" by an opaque, dark brown or charcoal-coloured area and the distal section containing ejaculate consistent with the description for "new only" (Figure 3.3).

3. **OLD ONLY** - Spermathecae containing only old, yellowish-beige spermatophores of a hard waxy consistency. Spermathecae appearing to be less full than those in the previous categories.

4. **NONE** - Spermathecae empty.

5. **UNKNOWN** - Spermathecae clearly not fitting any of the above categories.

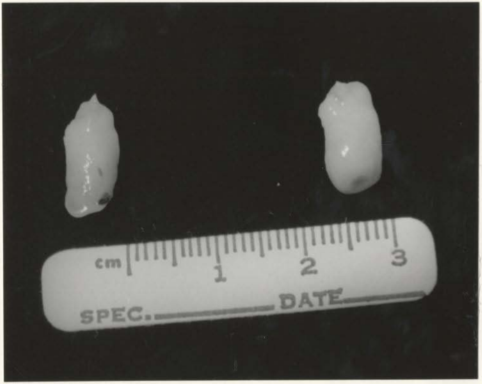

Figure 3.2: Spermathecae bearing new spermatophores only.

Figure 3.2: Spermathecae bearing new spermatophores only.

Grasping Mark Observations

Grasping marks were placed into four categories briefly described as follows and as illustrated in Figure 3.4:

1. **NEW ONLY** - Fresh, light coloured abrasions easily seen on the meri of the periopods of one or both sides of the body. No evidence of blackening of the shell caused by bacterial invasion of the chitin.

2. **OLD and NEW** - New grasping marks overlying old, blackened grasping marks from a previous mating.

3. **OLD ONLY** - Grasping marks consisting solely of old, blackened abrasions.

4. **UNKNOWN** - Abrasions that could not be categorized with certainty into the above categories.

5. **NONE** - No clear evidence of grasping marks.

Females classified in the "NONE" grasping mark group are most commonly primiparous. There might sometimes be an indentation on the periopods of these "NONE" category females suggesting that they had mated in the soft-shell

Figure 3.4: Legs of multiparous female depicting the three types of grasping marks. Uppermost leg bears new marks only, the middle leg bears old marks only while the lower leg bears both old and new marks.

condition but well-defined grasping marks similar to those observed on multiparous females are rarely present. Paul (1984) reported that primiparous *C. bairdi* mated in the laboratory usually did not bear grasping marks. Females without grasping marks were considered primiparous in the present study if they were new-shelled. It is also possible for old-shelled females to produce a second clutch using stored spermatophores from their primiparous mating which would not have left grasping marks. A recent laboratory study (Sainte-Marie and Carrière 1995) has demonstrated that this can occur quite frequently in *C. opilio*. Only females classified as having grasping marks on their periopods were included in the present study.

A small proportion of females with grasping marks did not have spermatophores in their spermathecae and these animals were excluded from the analysis because their recency of mating could not be determined. Soft-shelled females mated under both laboratory and field conditions have been observed to possess empty spermathecae despite bearing full egg clutches (personal observation). Paul (1984) found that the volume of spermatophores in the spermathecae shrinks with each successive fertilization of eggs and Sainte-Marie (1993) determined that after egg extrusion and fertilization the weight of the spermatophores within the spermathecae shrinks during storage. This fact combined with the observance of empty spermathecae in grasping-marked multiparous females suggests that the full spermathecal contents were used up either through a reduction in seminal fluids as the spermathecal contents aged (Sainte-Marie 1993) or through loss during fertilization.

RESULTS AND DISCUSSION

Potential Bias Due to Interactions Within Traps

The fact that trap-caught females have been confined for 24 hours or more with males raises the possibility that new grasping marks might result from trap interactions rather than actual mating encounters. This was evaluated by comparing trap-caught and trawl caught-females from offshore cruises (Figure 3.5) to see if there was a difference in the percentage of females bearing grasping marks between gear types.

Four cruises were conducted on the LADY HAMMOND between 1989 and 1992 during which mature females were examined to determine whether trap-caught females exhibited inflated percentages of recent grasping due to mating attempts while in the confines of the traps. Ovigerous females were captured both by commercial and small-meshed crab traps and by a Western IIA otter trawl which should have reduced these interactions. Data for both collection methods were

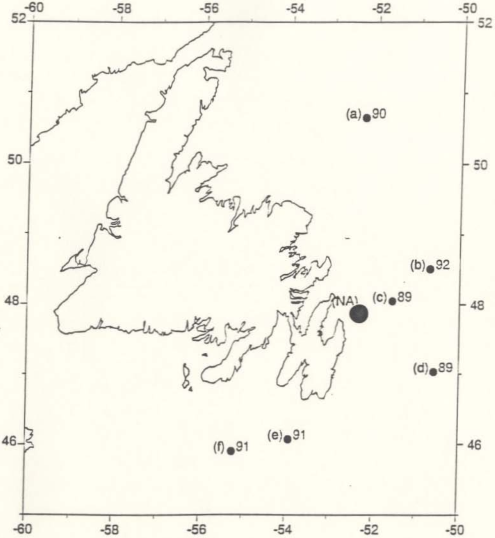

Figure 3.5: Location of offshore survey sites, 1989-92. "NA" and large solid circle denote Nearshore Avalon time-series sampling site. Lower case letters and small solid circles denote offshore sampling sites: a) Funk Island, b) Offshore Avalon, c) Offshore Avalon, d) Downing Basin, e) Haddock Channel and f) Halibut Channel.

analyzed separately in order to determine whether trap-caught females had a higher proportion of new grasping marks due to interactions within the trap during the soak period.

The results of this comparison (Table 3.1) show that 37.1% of the trap-caught new-shelled individuals bore new or new + old grasping marks, while 12.0% of the old-shelled females had new grasping marks. Of the trawl-caught individuals, 49.6% of the new-shelled females had new or new+old grasping marks while 30.3% of the old-shelled animals had new or new+old grasping marks. The fact that trawl-caught females had a significantly higher proportion bearing new grasping marks than did trap-caught females leads to rejection of the hypothesis of potential bias associated with the use of baited traps as a means of capture.

The observed results are the opposite of what would be expected if trap interactions were significant in contributing to misidentification of individual mating status. Differences must therefore have been the result of localized variation in actual mating despite the fact that trap samples were collected within a one nautical mile radius of the corresponding trawl sample.

In view of the fact that trap-caught females seem no more likely to bear "false" grasping marks than trawl-caught

Table 3.1: Comparison of efficacy of grasping marks as indicators of mating recency for offshore trap and trawl-caught females. Numbers in brackets are 95% confidence intervals calculated for the binomial distribution.

	NEW-SHELLED		OLD-SHELLED	
	GRASPING MARKS	PERCENT	GRASPING MARKS	PERCENT
TRAP	72 NEW+(NEW+ OLD)	37.1 (±6.9)	6 NEW+(NEW+ OLD)	12.0 (±9.2)
	122 OLD	62.9 (±6.9)	44 OLD	88.0 (±9.2)
TOTAL	194		50	
TRAWL	189 NEW+(NEW+ OLD)	49.6 (±5.1)	36 NEW+(NEW+ OLD)	30.3 (±8.4)
	192 OLD	50.4 (±5.1)	83 OLD	69.7 (±8.4)
TOTAL	381		119	

individuals, data from both gear types have been combined to provide a larger sample size for further analysis (Table 3.2).

Efficacy of External Classification of Mating Recency

The efficacy of classification of grasping marks as an indicator of mating recency/success can be determined by dissection of females and examination of their spermathecal contents. This was done both for the nearshore Avalon Peninsula commercial fishing grounds where ongoing time-series cruises have been conducted since 1979 and for opportunistic offshore cruises that sampled both heavily exploited areas and virgin or fully recovered areas.

Offshore Samples

The combined sample totals 747 females, 578 new-shelled and 169 old-shelled. Of the new-shelled females, 261 (45.2%) bore new grasping marks (Table 3.2), of which 204 also had fresh spermatophores in their spermathecae resulting in a recent mating prediction accuracy of 78.2%. The spermathecal contents of 4 individuals could not be classified. For the new-shelled females 316 (54.8%) possessed only old grasping marks and 216 of these possessed only old spermatophores, indicating that grasping marks as

Table 3.2. Summary of grasping marks and spermathecal contents for combined new and old-shelled trap and trawl-caught female snow crab.

NEW SHELL

Grasping Marks		Spermatophores		
		New + (New +Old)	Old	Unknown
New + (New + Old)	261	204	53	4
Old Only	316	95	216	5
Unknown	1	-	1	-
Total	578	299	270	9

OLD SHELL

Grasping Marks		Spermatophores		
		New + (New +Old)	Old	Unknown
New + (New + Old)	42	26	16	-
Old Only	127	16	111	-
Unknown	-	-	-	-
Total	169	42	127	-

an external predictor of mating recency/success was correct 68.4% of the time.

For the old-shelled females, 42 (24.9%) possessed new grasping marks and 26 of these also carried new spermatophores, indicating that the prediction based on the presence of new grasping marks was correct 61.9% of the time. The remaining 127 old-shelled females had only old grasping marks and 111 of these had only old spermatophores in their spermathecae. Thus the external classification was correct 84.7% of the time.

Avalon Peninsula Nearshore Samples

Spring trapping surveys conducted in the nearshore (<70 km from shore) Avalon area between 1987 and 1992 provide a long-term data record for evaluation of the efficacy of grasping marks as external mating indicators. Before 1987, grasping marks and spermathecal condition were not regularly sampled on these cruises. Females were grouped into new and old-shelled categories (see methods above) and then classified regarding recency of mating by external (grasping marks) and internal (spermathecae) examination (Table 3.3). A total of 884 new-shelled and 985 old-shelled individuals were examined. Of the new-shelled individuals, 484 (49.2%) were classified as having new or

Table 3.3. Grasping marks and spermathecal contents for trap-caught females from the Nearshore Avalon Peninsula, 1987-92.

NEW SHELL

Grasping Marks		Spermatophores		
		New + (New +Old)	Old	Unknown
New + (New + Old)	484	395	84	5
Old Only	399	126	273	-
Unknown	1	1	-	-
Total	884	522	357	5

OLD SHELL

Grasping Marks		Spermatophores		
		New + (New +Old)	Old	Unknown
New + (New + Old)	317	224	93	-
Old Only	666	156	510	-
Unknown	-	-	-	-
Total	983	380	603	

new + old grasping marks combined. Internal examination revealed that 395 (81.7%)of these newly-grasped females had new or new + old spermatophores in their spermathecae and thus were correctly classified externally while 5 had spermathecal contents that could not be classified ("Unknown"). The remaining 399 new-shelled females were classified as having old grasping marks only and 273 of these (68.4%) carried old spermatophores only while the rest carried either new or new and old spermatophores. These two errors were partially compensatory, with the result that the grasping-mark-based prediction of 484 newly-mated females was very close to the internal examination results which indicated 521 females carried new spermatophores.

Classification of old-shelled females mating status was less accurate than new-shelled with 224 of the 319 females (70.2%) classified as having new grasping marks actually possessing new spermatophores upon internal examination. In contrast, 510 of the 666 females classified on the basis of external examination as only having old grasping marks actually possessed old spermatophores only (76.6% correct). The net result was that 319 were predicted to have recently mated on the basis of external grasping mark classification compared to 380 that were found to have recently mated based on the classification of spermatophores in the spermathecae.

These data can also be used to compare the mating frequency of mature females on the basis of shell condition. New-shelled individuals had a higher level of recent mating activity than old-shelled females. Of the 985 old-shelled females only 38.6% (380) had new spermatophores whereas 59% of the new-shelled females had new spermatophores (552 of 884). In terms of external classification, only 32.4% of the old-shelled females had new or new and old grasping marks as compared to 49.2% of the new-shelled females.

Overall, external indicators of mating success produced recent mating estimates that were only 10% too low for new-shelled females and 20% too low for old-shelled individuals. This degree of accuracy may be sufficient to permit comparison of apparent mating recency among various areas or to make among year comparisons for the same area.

There remains the possibility that even visual examination of the spermathecae can sometimes be misleading. Elner and Beninger (1989) found that only one of 16 females from eastern Cape Breton Island with visibly distended spermathecae actually had spermatophores in the matrix when examined microscopically. In contrast, Ennis et al. (1989) documented that each of twelve females from a Bonne Bay sample visually classified as carrying new or new + old spermatophores did indeed have spermatophores in the spermathecal matrix when the contents were histologically prepared and examined microscopically. The reasons for these discrepancies between areas remains unknown.

Comparison of the Efficacy among Nearshore and Offshore Populations

The efficacy of utilizing grasping marks as a means of determining mating recency/success varied little between nearshore and offshore sampling areas. Nearshore, classification of new-shelled, newly-grasped females correctly predicted spermathecal content 81.7% of the time, while offshore prediction for the same group were 78.2% correct. Predictions for new-shelled nearshore females bearing old grasping marks were correct 68.4% of the time while predictions for new-shelled offshore females with old grasping marks only were also correct 68.4% of the time. Nearshore old-shelled females classified as having new grasping marks had new spermatophores in their spermathecae 70.2% of the time versus 61.9% for offshore old-shelled females with new grasping marks while nearshore old-shelled females bearing old grasping marks, only were correctly predicted 76.6% of the time compared to 84.7% for those from offshore samples. Thus it would appear that using grasping marks as a predictor of mating success/recency works reasonably well whether sampling nearshore or offshore areas and whether utilizing baited traps or otter trawls. Although the possibility that "grasping marks" may in some cases be due to interactions other than the mating embrace, the severity of the abrasions and location of them on females, periopods make other causes for their presence unlikely.

SUMMARY

The results of the investigation into the utility of grasping marks as indicators of mating recency can be summarized as follows:

1: Grasping marks associated with pre-copulatory and copulatory behavior of mating snow crabs serve as a relatively accurate indicator of mating recency/success in multiparous female snow crabs.

2: Grasping marks can be utilized for both trap-caught and trawl-caught multiparous females. Trap-caught females do not appear to bear false grasping marks as a result of male/female interactions within a trap.

3: New-shelled multiparous females have a higher recent mating rate than do old-shelled females.

Chapter 4: General Discussion and Summary

Fecundity of Virgin Versus Heavily Exploited Areas

While a reduction in the percentage of ovigerous mature females has been reported from heavily exploited areas (Elner and Robichaud 1986; Taylor and O'Keefe 1986) the impact of exploitation on individual fecundity has not previously been investigated. The results of the present study indicate that females from the virgin areas of Newfoundland had a significantly higher level of fecundity than did those from exploited areas both in terms of egg number and mass. Multiple regression analysis of all areas combined revealed significant size-specific fecundity differences related to spermatophore type and, to a lesser degree, age as represented by shell condition. Residual significant differences between size-specific fecundity in virgin and exploited areas are not yet attributable to specific biological or physical factors.

One explanation for the observed differences is that a male-only fishery may reduce the ratio of males to females below the level at which all females can be serviced during a breeding season. Paul (1984) demonstrated in a laboratory study of *C. bairdi* that female/male ratios above 8:1 resulted in a significantly increased proportion of multiparous females utilizing stored sperm to fertilize their eggs. This resulted in lower fecundity due to the failure of some females to produce fertilized egg clutches. While the negative effects were small (<3%) for females producing their second egg clutch from stored sperm, only 71% of those forced to fertilize a second clutch from the same sperm produced full clutches and 9% of these were comprised of dead eggs. This strongly suggests that the viability of stored spermatophores decreases over time. Primiparous *C. bairdi* are less successful in utilizing stored sperm to fertilize second clutches of eggs than are multiparous females. Paul and Paul (1992) found that only one of eleven primiparous females (9%) received enough spermatophores from their initial mating to fertilize a second clutch of eggs. A recent laboratory study by Sainte-Marie and Carrière (1995) suggests, however, that primiparous *C. opilio* females using stored sperm to fertilize a second clutch have a much higher degree of success (88%, based on a simple clutch fullness index) than did the primiparous *C. bairdi* females. They caution that their findings cannot be indiscriminately extrapolated to wild populations. The spermatophore effect observed in the present study (Chapter 2) in which females using old sperm had significantly lower size-specific fecundity than those using new sperm, is consistent with these laboratory observations.

Elner and Robichaud (1986) reported that the number of berried females on the Atlantic coast of Cape Breton was sharply reduced following a dramatic decline in the availability of large males. They speculated that the decline in the incidence of berried females could have resulted from the reduction of sexually competent males through losses to the commercial fishery. Further to this, McMullen and Yoshihara (1971) and Smith and Jamieson (1991) suggested that male fishing mortality and resultant reduction in suitable males could contribute to female infertility in some red king (*Paralithodes camtschaticus*) and Dungeness crab (*Cancer magistar*) populations in Alaska and British Columbia respectively. There were relatively few instances in the present study in which the proportion of berried females fell below 90% (see Table 2.2) despite very high exploitation rates.

The size of males attempting to mate with multiparous females has also been reported as an important factor affecting breeding success for *C. bairdi* (Adams 1982, Paul and Paul 1996) and *C. opilio* (Conan and Comeau 1986). Both studies reported that small males experienced difficulty in mating with multiparous females. The mean size of males captured concomitantly with the females in the present study did not appear to be correlated with size specific fecundity differences (Figure 2.5 in Chapter 2). The actual size of successfully mating males was unknown, however.

Regional Comparisons of Fecundity

Fecundity of *C. opilio* and its congeners has been examined by various authors both on the Atlantic (Brunel 1962; Powles 1968; Haynes et al. 1976; Thompson 1979; Elner and Gass 1983; Davidson et al. 1985; Sainte-Marie 1993) and Pacific coasts (Kon 1974; Haynes et al. 1976; Jewett 1981; Somerton and Meyers 1983). With only one exception (Elner and Gass 1983), fecundity (in terms of numbers of orange, recently extruded eggs carried attached to the pleopods) was found to be positively correlated with size measured as carapace width (CW). Overall, fecundity in the Northwest Atlantic ranged from 12,000 to 128,000 (Elner and Beninger 1992). Fecundity regressions for most studies including the present one are summarized in Table 2.1 and plotted in Figure 4.1. Fecundity of Newfoundland snow crab calculated from data collected for this study confirm Elner and Robichaud's (1983) conclusion that Newfoundland snow crab are less fecund for a given size than all other Northwest Atlantic populations. Interestingly, the fecundity curve generated by Davidson et al. (1985) for Newfoundland snow

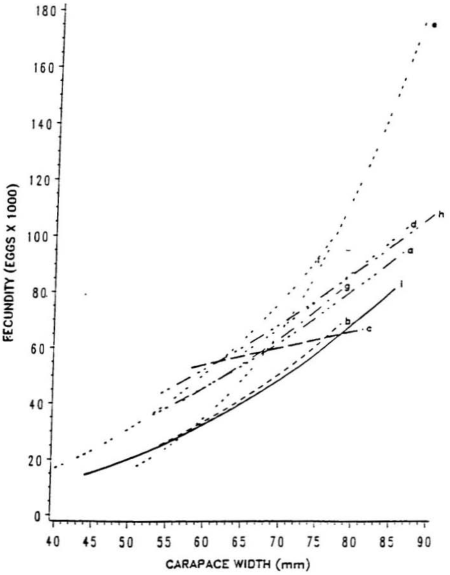

Figure 4.1: Size-fecundity regressions for female snow crab from Newfoundland compared with other North American study areas: a) Anticosti Island, b) Bering Sea, c) Cape Breton, d) Gabarus, e) Gulf of St. Lawrence, f) Baie Sainte-Marguerite, g) Newfoundland 1981, h) Pleasant Bay and i) present study.

crab captured in the nearshore Avalon area in the spring of 1981, demonstrates a higher size-specific fecundity than that for females in the present study that were captured during 1984-85. For example, the earlier fecundity regression predicts a 55 mm (CW) female will carry 38,157 eggs while the predictive regression from the present study for the same area yields only 23,852 eggs. Even the fecundity regression corrected for virgin area effect predicts that a 55 mm (CW) female will carry only 28,684 eggs. The area specific prediction for the Downing Basin, where females had the highest size-specific fecundity recorded in this study was 31,305 eggs which is still well below the prediction from Davidson et al. (1985). This suggests that there may be additional temporal trends in size-specific fecundity worthy of future research.

Recruitment of mature females may also be affected by variability in larval survival and the survival of small juveniles in the cryptic stage of their life cycle (Lovrich and Sainte-Marie 1995). In view of this, management strategies should protect multiparous females and ensure high mating success by maintaining a suitably large population of functionally mature males.

Relation of this Study to Snow Crab Management Strategy

Recruitment to sexual maturity requires molting which is unpredictable and may be subject to temperature (Taylor et al. 1994) or density effects (Ennis et al. 1990) or may display cyclical patterns (Sainte-Marie et al., in press). Although there is no doubt that primiparous females can make a significant contribution to the reproductive output of snow crab populations during periods of high recruitment (Sainte-Marie 1993), the dependence on primiparous fecundity as a mainstay of population reproductive potential is a risky management strategy. The instability of yearly recruitment (Bailey and Elner 1989), sudden and prolonged failures of the molting cycle (Taylor et al. 1994) or the existence of an inherent cyclicity resulting in three years poor recruitment following five years of good recruitment (Sainte-Marie et al. in press) all demand that measures be taken to ensure that there are sufficient large males left in an area to fertilize multiparous females. If natural mortality of multiparous females is low and prudent female discard practices are followed by fishers, multiparous females should contribute a more consistent reproductive output over time to a population. The results of the present study indicate that the reproductive contribution of multiparous females can be negatively affected by extreme fishery exploitation. This seems in part the result of reduced mating frequency and consequent greater reliance on old spermatophores for fertilization (resulting in decreases in fecundity Chapter 2). It thus is probably prudent to examine the fecundity of multiparous females in exploited populations on a regular basis in order to determine whether the proportion successfully mating each year is changing. Sudden and dramatic increases in the percentage of multiparous females utilizing stored spermatophores might indicate excessive exploitation rates accompanied by a decline in large sexually-competent males.

Efficacy of Grasping Marks as Indicators of Mating Recency

The results of this study clearly demonstrate that grasping marks have the potential to provide the basis for quickly determining the reproductive status of multiparous females during research surveys whether using baited traps or trawls as sampling tools.

Although grasping marks have been used to a limited degree in Bonne Bay, Newfoundland as indicators of mating success of male/female pairs participating in the annual mating migration from deep to shallow water in that area (Taylor et al. 1985; Ennis et al. 1988) their utility as a survey tool in commercially exploited areas has not been tested until this study. In the present study grasping marks correctly predicted the mating status of multiparous females approximately 70-80% of the time as confirmed by dissection and spermathecal examination. Errors for new and old grasping marks in terms of correctly predicting spermathecal contents were similar in magnitude thus effectively cancelling each other out and making the utility of grasping marks even more promising.

Routine examination and classification of grasping marks on multiparous females could thus provide an early warning of scarcity of sexually competent males which might then trigger in-depth fecundity observations.

SUMMARY

The results of this study can be summarized as follows:

1. The observed percentage of berried females in snow crab populations usually was high (>90%) and was largely independent of the commercial exploitation rate.

2. Size-specific fecundity of females in virgin areas was higher than that of those in commercially exploited areas. This higher level of fecundity was related to spermatophore type from which it can be inferred that recency of mating affects fecundity, i.e. females utilizing new spermatophores are more fecund than those relying on old spermatophores.

3. This enhanced fecundity bestowed by new spermatophores suggests that a rapid method of assessing recency of mating might be useful in comparing snow crab populations' reproductive health.

4: Grasping marks associated with pre-copulatory and copulatory behavior of mating snow grabs serve as an accurate indicator of mating recency/success in multiparous female snow crabs.

5: Grasping marks can be utilized for both trap-caught and trawl-caught multiparous females. Trap-caught females do not appear to bear false grasping marks as a result of male/female interactions within a trap.

6: New-shelled multiparous females have a higher recent mating rate than do old-shelled females.

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Appendix A: Size-frequency distribution of males caught concomitantly with females examined in this fecundity study.

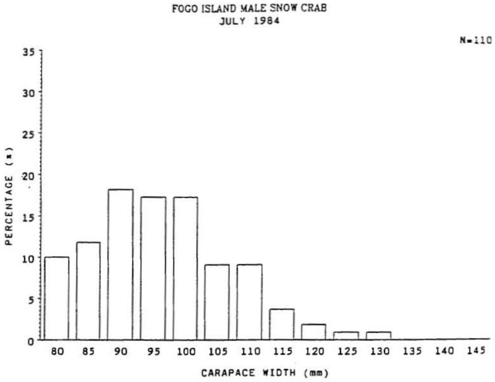

Figure A1: Size-frequency distribution of males from Fogo Island caught concomitantly with females examined in this fecundity study.

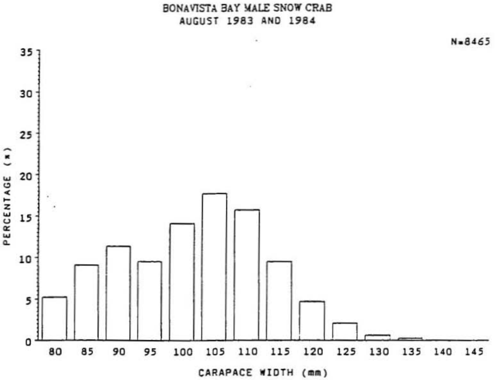

Figure A2: Size-frequency distribution of males from Bonavista Bay caught concomitantly with females examined in this fecundity study.

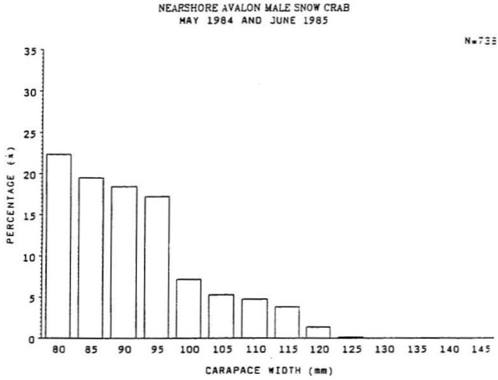

Figure A3: Size-frequency distribution of males from Nearshore Avalon caught concomitantly with females examined in this fecundity study.

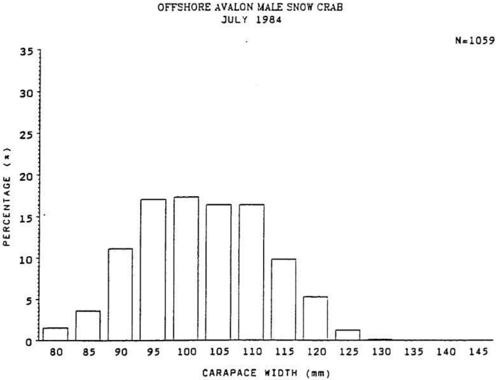

Figure A4: Size-frequency distribution of males from Offshore Avalon caught concomitantly with females examined in this fecundity study.

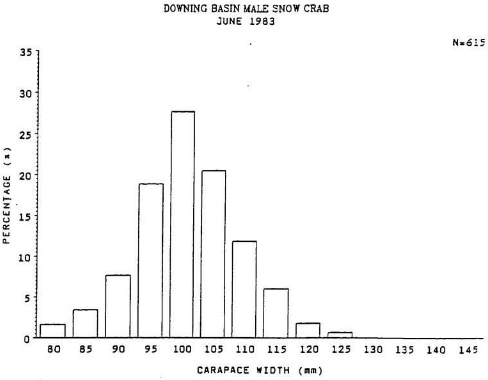

Figure A5: Size-frequency distribution of males from Downing Basin caught concomitantly with females examined in this fecundity study.