Molt Increments, Annual Molting Probabilities, Fecundity and

Survival Rates of Adult Female Dungeness Crabs in Northern

California.

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Introduction

Although the Ricker stock-recruitment, Leslie matrix and other models of population dynamics are often formulated exclusively in terms of females, studies of the Dungeness crab (Cancer magister) have concentrated almost exclusively on male crabs. Failure to devote research attention to female crabs is undoubtably explained by the facts that commercial female harvest is prohibited in most West Coast fisheries (only British Columbia allows commercial harvest of females that exceed legal size for males), and that females are smaller and have less commercial value or potential value than do males. However, as the models suggest, females are normally regarded as the more important sex from a population dynamics perspective and, in the usual fishery context, should receive more research attention than males rather than less. This is particularly true for a polygamous species such as the Dungeness crab, where very few adult males may ensure insemination of virtually all adult females (PMFC 1978; Poole and Gotshall 1965).

McKelvey et al. (1980), assuming an underlying endogenous explanation, showed that fluctuations in landings of male Dungeness crabs in the northern California fishery could be most plausibly explained by density-dependent egg/larval survival mediated through fluctuations in total egg production of the unexploited female stock (see Hankin, this Symposium, for a critique of this and other hypotheses). Because their conclusions rested on extremely tentative data concerning age and growth, fecundity and survival rates of adult female Dungeness crabs, they recommended that study of the demographic statistics of female Dungeness crabs receive immediate and priority attention.

This paper presents the principal results of a three year California Sea Grant-sponsored project specifically designed to allow determina-

tion of the vital demographic statistics of adult female Dungeness crabs in northern California. Research consisted primarily of a tag-recovery project in which more than 12,000 adult female crabs were tagged and released, laboratory generation of molt increments from 185 females removed from pre-mating embraces, and estimation of total fecundity of 122 adult female crabs. From results of these studies, we have been able to paint a remarkable picture of the life history of adult female Dungeness crabs. In particular, we found strong size-dependence of molt increments, molting probabilities, fecundity and survival rates; such dependence was often unexpected. Among females exceeding 155 mm carapace width, fecundities were often low (200-400,000 eggs), annual molting probabilities were effectively zero, and annual survival rates were about 10%; these figures were far less than those for smaller younger adult female crabs (125-135 mm carapace width). Based on these findings, and other bits of evidence, we present an argument for senescence among adult female Dungeness crabs.

The intention of this paper is to present a concise descriptive review of the more significant of our findings. As a consequence, details of certain methodologies are only briefly sketched or occasionally omitted so as to present an overall perspective of the life history of adult female Dungeness crabs within the confines of a single brief paper. Where appropriate, reference is made to existing and/or contemplated documents in which relevant details may be found. We hope that this obvious sacrifice of completeness of detail is more than compensated for by the reader's ability to quickly and easily grasp our principal findings.

Materials and Methods

The northern California commercial fishery for male Dungeness crabs opens 1 December and runs through 30 July (unless extended through August by California Fish and Game). Thus, a single commercial season spans two calander years. Project activities were necessarily closely linked with the commercial fishing season, in part because all field research took place on board a contracted commercial crab fishing vessel out of Trindad, California, and because most tag recoveries were received from cooperating commercial fishermen, but also because of Dungeness crab life history. In particular, ovigerous female Dungeness crabs are most frequently captured in traps during the months of December and January. To simplify presentation of methods and results, where it would otherwise be awkward to mention two calander years, project "years" have been defined as twelve month periods beginning   1 December of 1980, 1981 and 1982. Thus, for example, the first project year spanned the period 1 December 1980 through 30 November 1981. An additional convention involves the use of the term "large" in reference to the size of female crabs; "large" will consistently refer to female crabs of carapace width ≥ 155 mm.

More than 12,000 adult female crabs ranging in carapace width from about 85 to 172 mm were tagged and released between the mouth of the Mad River (40° 55' N) and Freshwater Lagoon (41° 15' N) during the months of January through March of 1981-1983 at depths of 10-24 fathoms (18-44 m). (See Diamond and Hankin, this Sympsoium, for site maps and detailed descriptions of release locations). Crabs were measured to 0.1 mm across the widest part of the carapace (excluding the tenth anterolateral spines), and were tagged at the posterior epimeral suture with numbered FLOY anchor tags (Model FD-68B).

During 1983 tagging activities a qualitative assessment of molting history of each tagged crab was made based on visual examination of carapace condition (degree of fouling, blackening around joints, etc.)... Crabs were classified as (a) molted during most recent molting season, (b) uncertain molt history, or (c) failed to molt during most recent (and possibly previous) molting season(s). Recoveries were received primarily from commercial fishermen, although small numbers were recovered during tagging activities. Recovery data provided by fishermen included date, depth and location (LORAN-C reading or coastal landmark) of recovery. Because commercial crab traps in northern California have large mesh size (70-100 mm on diagonal) and two ≈ 10.3 cm diameter escape ports, recoveries of tagged crabs by commercial fishermen were biased toward larger crabs by trap size selection. To allow statistical adjustment for such bias, and to allow capture and tagging of small adult females (100-135 mm), specially designed crab traps, which were non-selective above about 85 mm carapace width, were fished parallel with commercial trap gear. (See Diamond 1983; Diamond and Hankin, this Symposium, for details regarding trap size selection and modified experimental traps.)

During late April through early June of 1981 and 1982 (when female molting and mating takes place in northern California), the contracted commercial fisherman and his crew collected females from pre-mating embraces for us. (Females are found paired with males in such embraces just prior to female molting; when the female molts, the hard-shelled male mates with the soft-shelled female in the true mating embrace.) These females were brought to the Telonicher Marine Laboratory in Trindad where they were held until molting took place, usually within four days. Premolt and postmolt carapace widths were recorded for 185 such females which molted in the Laboratory.

Most ovigerous females were collected during late December through early January of the second and third project years from traps fished from the contracted vessel; additional recoveries of tagged ovigerous crabs were received at the Telonicher Marine Laboratory. Collected females carried eggs which were usually bright orange in color and at an early stage of development, well before the eyed stage and larval release. Females were immediately placed in Bouin's fluid, on board the vessel or at the Laboratory, so as to minimize physical damage to egg masses; live ovigerous females tend to physically "tear" at their own egg masses when handled. Female   widths were measured, molting condition was assessed as described above or known from tag-recovery records, and egg masses were removed from females and transferred to fresh Bouin's fluid in which they remained for about one month prior to processing. Processing consisted of a drying and cleaning protocol which resulted in production of a small volume of dried, cleaned, hardened and separated eggs. For the second year's collections, at least six random 0.020 g subsamples were counted from each dried egg mass. Total fecundities and variances of estimated fecundities were estimated using a mean-per-unit estimator (Cochran 1977). For third year collections, only a portion of collected specimens were actually subsampled (8 subsamples of 0.020 g each), but all specimens were processed to produce dried egg masses. For those egg masses for which estimates were not based on subsampling, total fecundities and variances of estimated fecundities were estimated from dried egg mass weight based on a regression of estimated total fecundities against dried egg mass weight among subsampled specimens. This statistical procedure allowed us to minimize subsampling effort and expand the

number of specimens for the third project year. Details of sample preparation and statistical analyses will be presented in Hankin and Ianelli (in prep.).

A total of 362 female crabs were collected in non-selective traps during late May of 1983 and were classified as (a) recently molted, or (b) failed to molt during most recent molting season, according to visual examination of carapace condition. Because the molting season had only just concluded by late May of 1983 (Mohr, unpublished), visual assessment of molting history was most accurate at this time of year. Recently molted females could be readily distinguished from those that had failed to molt.

Linear regressions were used to describe the relations between molt increments and premolt carapace widths for tag-recovery data and for data generated from pre-mating embrace females that molted in the Laboratory. Techniques for comparison of regression lines (Snedecor and Cochran 1967) were used to compare tag-recovery and Laboratory/pre-mating embrace regression lines so as to examine the effects of tagging on molt increments. Annual molting probabilities for adult females were estimated using two independent methods. Estimators which accounted for biases due to tag loss and commercial trap size selection were developed and applied to tag-recovery data. For these analyses, only those crabs which (a) were released prior to 1 April and (b) were recovered after 1 June of the year of tagging but before 1 April of the following year were included in analyses. This restricted analyses to those crabs which should have had just a single opportunity to molt. Details of tag-recovery-based molting probability estimators are presented in Diamond (1983) and Diamond and Hankin, this Symposium. An independent estimator developed by Mohr (unpublished) was applied to shell condition data collected during late May of 1983 and to analagous data collected during tagging activities in January of 1983. Multiple regressions, with molting history as a dummy variable (Draper and Smith 1981), were used to statistically account for the variation in total fecundity as a function of carapace width and molting history. All tests of statistical significance were made at 5%. Finally, survival rates for large adult female crabs (those ≥ 155 mm carapace width) were estimated from the sequence of recoveries of crabs tagged in each of the three project years following techniques presented in Brownie et al. (1978, Model 1) and Youngs and Robson (1975). Survival rates for smaller crabs could not be directly estimated, but qualitative comparison of recovery sequences for smaller crabs allowed inference of relative survival rates as compared with larger crabs.

Results

Of more than 12,000 adult female crabs which were tagged and released, just over 600 crabs were recovered as of 31 August 1984. Overall recovery rate was about 5%, but recovery rates were strongly size-dependent and reflected commercial crab trap size selection. For adult females ≥ 155 mm carapace width, recovery rates were about 11%; for females falling between 124 and 136 mm recovery rates were only about 2.5%. Of the total recoveries, 289 had been at large through a single molting season and could be used for tag-recovery-based estimators of annual molting probabilities; 111 of these had molted and could be reliably used for molt increment regressions (Table 1).

Table 1. Total number of female Dungeness crabs tagged and
recovered by size (as of 31 August 1984).

Mid-Point (mm)	Numbers Tagged	Numbers Recovered
86.5	3	0
89.5	0	0
92.5	2	0
95.5	4	0
98.5	1	0
101.5	6	0
104.5	12	0
107.5	23	0
110.5	43	0
113.5	75	2
116.5	131	1
119.5	215	4
122.5	301	4
125.5	491	5
128.5	611	9
131.5	782	28
134.5	918	32
137.5	1139	43
140.5	1242	52
143.5	1383	56
146.5	1148	49
149.5	922	43
152.5	915	87
155.5	768	76
158.5	497	57
161.5	253	32
164.5	119	23
167.5	27	3
170.5	8	1
Totals:	12037	607

Molt increments.

Molt increments declined linearly with increasing female carapace
width for both tag-recovery and laboratory/mating embrace data.
Molt increments for adult females of 100 mm averaged about 19 mm,
whereas molt increments for females of 150 mm averaged about 12
mm. Regression lines of molt increments against premolt size were
not significantly different between tag-recovery and laboratory-genera-
ted data, thus suggesting that tagging had no statistically significant
effect on molt increments of released crabs (Figures 1 and 2).
Variation about the molt increment regression (Figure 2) was approxi-
mately constant over the full range of premolt carapace widths.

Molting probabilities

A total of 289 crabs was recovered after a single molting season at
large, of which only 111 had molted. Failure to molt was most evident
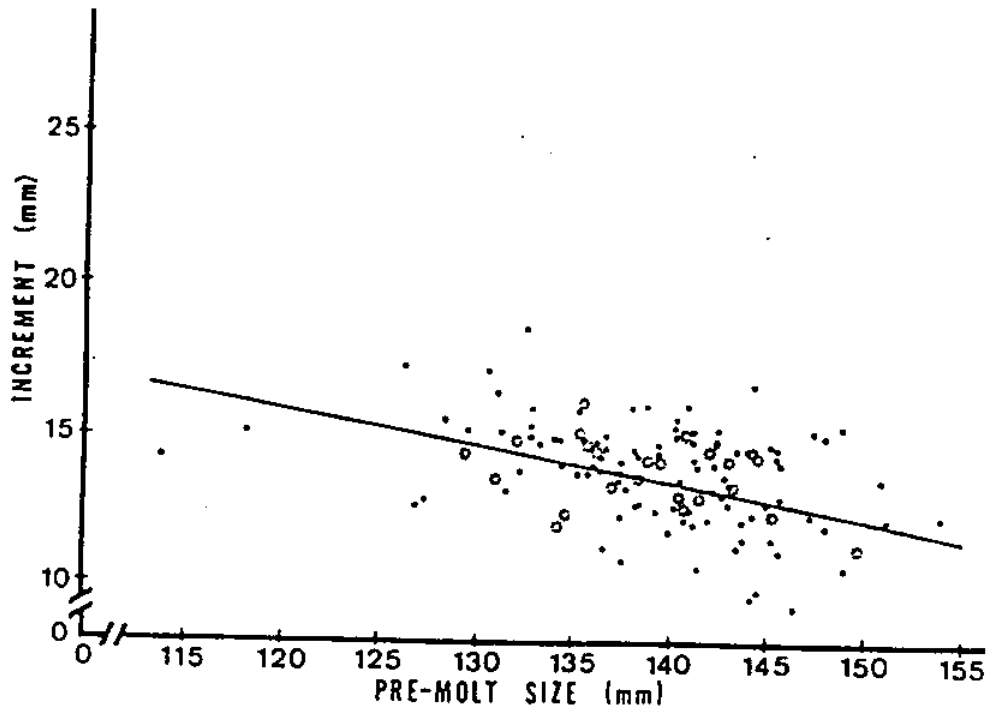among larger female crabs (Table 2). A total of 53 crabs was recovered

Figure 1. Molt increments plotted against pre-molt carapace widths. Solid symbols - recoveries of molted crabs at large through a single molting season. Open symbols - recoveries of crabs at large through two molting seasons, but which molted only once. Solid line indicates regression of increment against pre-molt size for solid symbols.
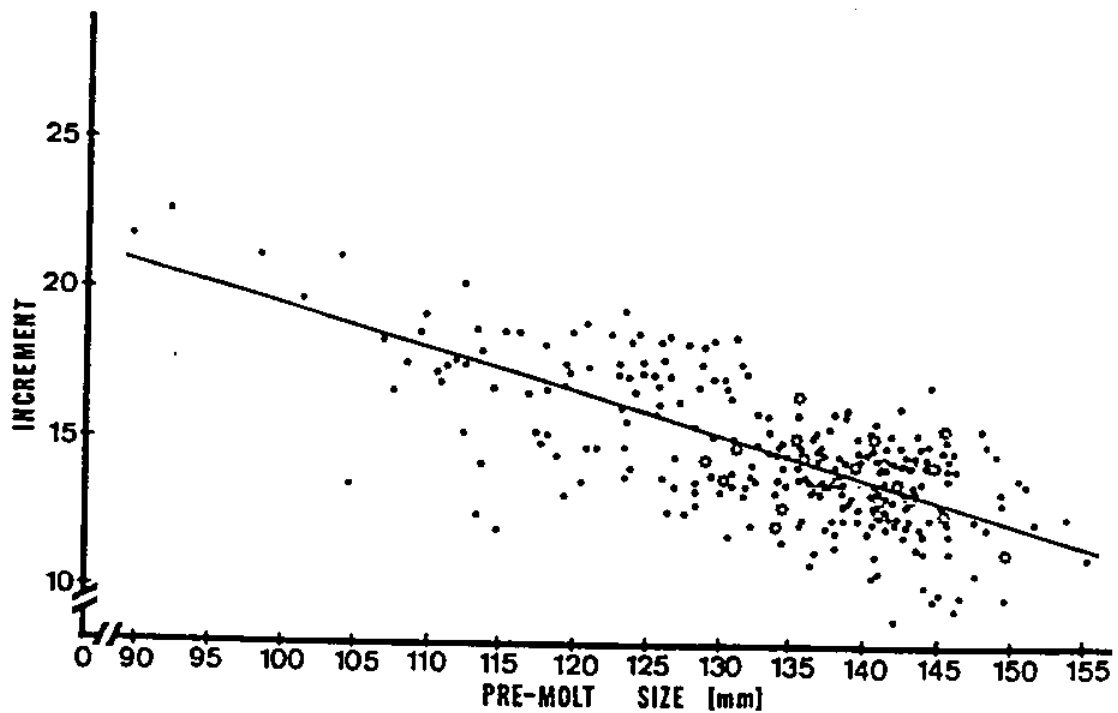

Figure 2. Molt increments plotted against pre-molt carapace widths for tag-recovery and laboratory/mating embrace data combined. Solid circles and open symbols as for Figure 1; asterisks are for laboratory-generated data. Solid line shows regression line for combined data, solid symbols only.

Table 2. Recoveries of tagged crabs at large for a single molting
season. Size indicates carapace width at tagging.

Mid-Point (mm)	Not Molted	Molted	Total Recovered
113.5	0	1	1
116.5	0	1	1
119.5	1	1	2
122.5	0	1	1
125.5	1	3	4
128.5	2	3	5
131.5	5	11	16
134.5	4	9	13
137.5	7	21	28
140.5	8	18	26
143.5	11	21	32
146.5	16	14	30
149.5	17	4	21
152.5	28	3	31
155.5	25	0	25
158.5	26	0	26
161.5	11	0	11
164.5	12	0	12
167.5	3	0	3
170.5	1	0	1
Totals:	178	111	289

after having been at large through two molting seasons. Again, fre-
quency of molting was greater for smaller crabs than for larger crabs
and double molts were evident for a few small crabs (Table 3). Reco-
veries of crabs that had been at large through three molting seasons
have been few, but displayed the same trends as seen in Tables 1 and
2; molting was more frequent among smaller crabs (Table 4). For
large crabs (those ≥ 155 mm carapace width), total recoveries have
been 80: of these, 79 were recovered after one molting season at
large and one was recovered after two molting seasons at large. None
had molted.

Data presented in Tables 2-4 are, as previously mentioned, biased by
size selection in the commercial fishery recovery gear. A naive cal-
culation, which would calculate annual molting probability simply as
the fraction of recoveries which returned molted for a particular size
interval at tagging, would show a steep decline in molting probabilities
from about 135 mm through 155 mm; beyond 155 mm molting probabili-
ties were effectively zero. However, these calculations would be (a)
positively biased by trap size selection (a crab that molted to a larger
size would be more likely to be recovered than would a crab of the
same initial size that had failed to molt), and (b) negatively biased by
tag loss through the molt (a crab which loses its tag while molting
obviously cannot be recovered). The combined effect of these two
biases is unclear, although we suspect that the principal effect is a
positive bias in molting probabilities estimated via the naive calculation.
Figure 3 shows results of applying the developed molting probability
estimators to (a) tag-recovery data and (b) shell condition data, as
well as the naive calculations. Estimates derived by the three methods

Table 3. Recoveries of tagged female crabs at large through two molting seasons. "-?-" indicates uncertainty regarding one or two molts based on increment from tagging to recovery.

Mid-Point (mm)	No Molt	One Molt		Two Molts	Total Recovered
113.5	0	0		1	1
116.5	0	0		0	0
119.5	0	0		0	0
122.5	0	0		1	1
125.5	0	0		1	1
128.5	0	2		0	2
131.5	0	6	-?-	0	7
134.5	0	5	-?-	0	6
137.5	0	6		0	6
140.5	0	7		0	7
143.5	2	8		0	10
146.5	1	5		0	6
149.5	0	2		0	2
152.5	3	0		0	3
155.5	0	0		0	0
158.5	0	0		0	0
161.5	1	0		0	1

Table 4. Recoveries of tagged female crabs at large through three molting seasons.

Mid-Point (mm)	No Molt	One Molt	Two Molts	Total Recovered
119.5	0	0	1	1
122.5	0	0	2	2
125.5	0	0	0	0
128.5	0	1	1	2
131.5	0	0	0	0
134.5	0	3	0	3
137.5	0	1	0	1
140.5	0	4	0	4
143.5	0	1	0	1

are not in agreement, but all suggest a pattern of rapid decline in annual molting probabilities (beginning somewhere between 130 and 135 mm carapace width) to effectively zero for crabs with carapace widths in excess of 155 mm.

Fecundity.

Estimated total fecundities of 35 female Dungeness crabs collected during the second project year are presented in Figure 4. Total fecundity was not significantly linearly related to carapace width for these data. Failure to discover a significant increasing trend of total fecundity with increasing carapace width prompted a more extensive fecundity sampling program during the third year. Expanded sample size was made possible by the discovery that total fecundity estimates derived by subsampling were highly correlated with dried egg mass
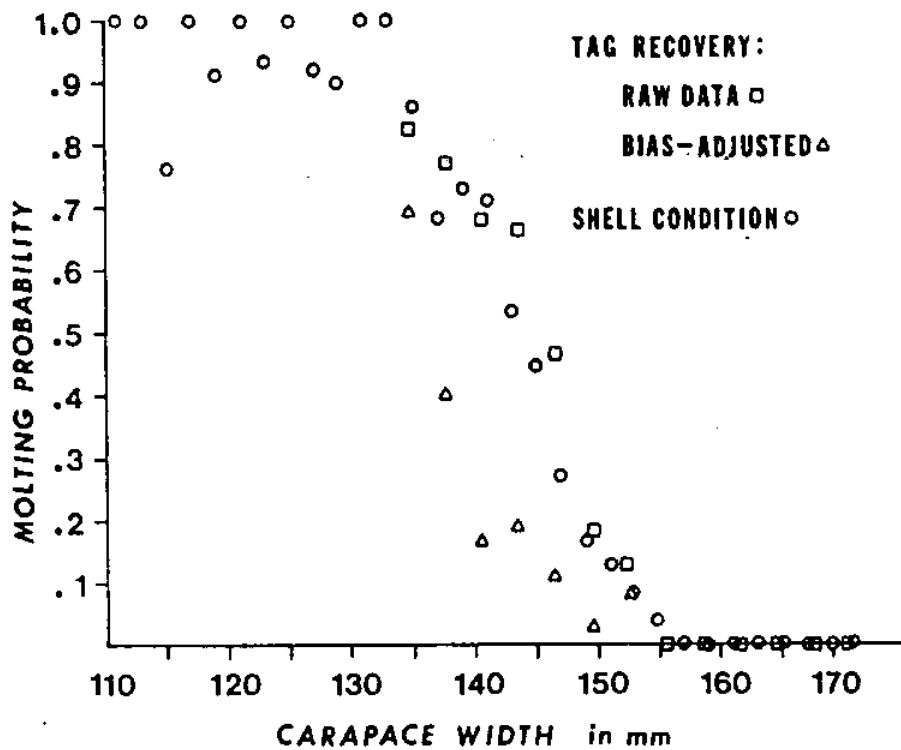
Figure 3. Estimated annual molting probabilities for female Dungeness
crabs plotted against female carapace width. "RAW DATA"
= naive calculations described in text; "BIA-ADJUSTED" =
estimates based on tag-recovery data, adjusted for gear
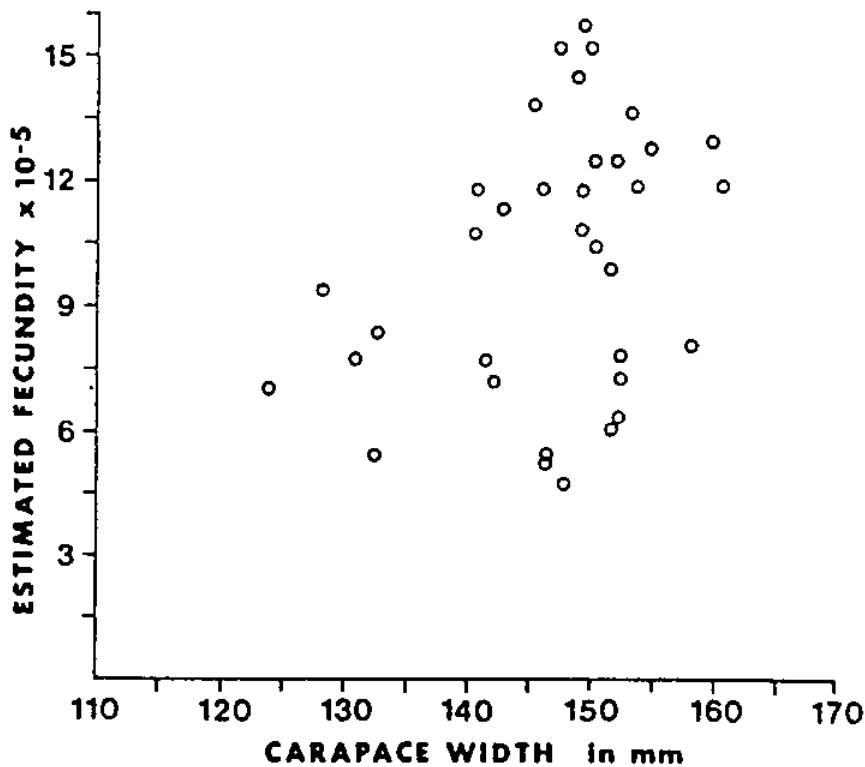selection and tag loss.

Figure 4. Estimated total fecundity plotted against carapace width for
specimens collected during the second project year. All
estimates are based on subsampling of dried egg masses.

weights (Figure 5). Confidence intervals based on subsampling were always within ± 10% of the estimated total; those derived from the regression of estimated total fecundity against dried egg mass weight were roughly ± 100,000 eggs and, for most specimens, were between ± 10-20% of the estimated total. Apparent variation in size-specific fecundity was therefore real and not a result of estimation methods; errors of estimation were small compared to size-specific variation among estimated fecundities. Combined fecundity estimates for the second and third project years are plotted on Figure 6 as are estimates for ten California crabs collected from the Farallone Islands which appear to belong to the same set of data (Hines, pers. comm.). Clearly, fecundity was only weakly related to female carapace width in both years' collections. A regression of total fecundity against carapace width was significant for the third year's data, but could explain only about 6% of the total variation in estimated fecundity. It is worth noting that variation among these data is far greater than among those data presented in Mayer (1973) for Washington crabs; however, Mayer had no crabs exceeding 145 mm carapace width.

$$\hat{Y} = 12,741 + 54,533\,X$$

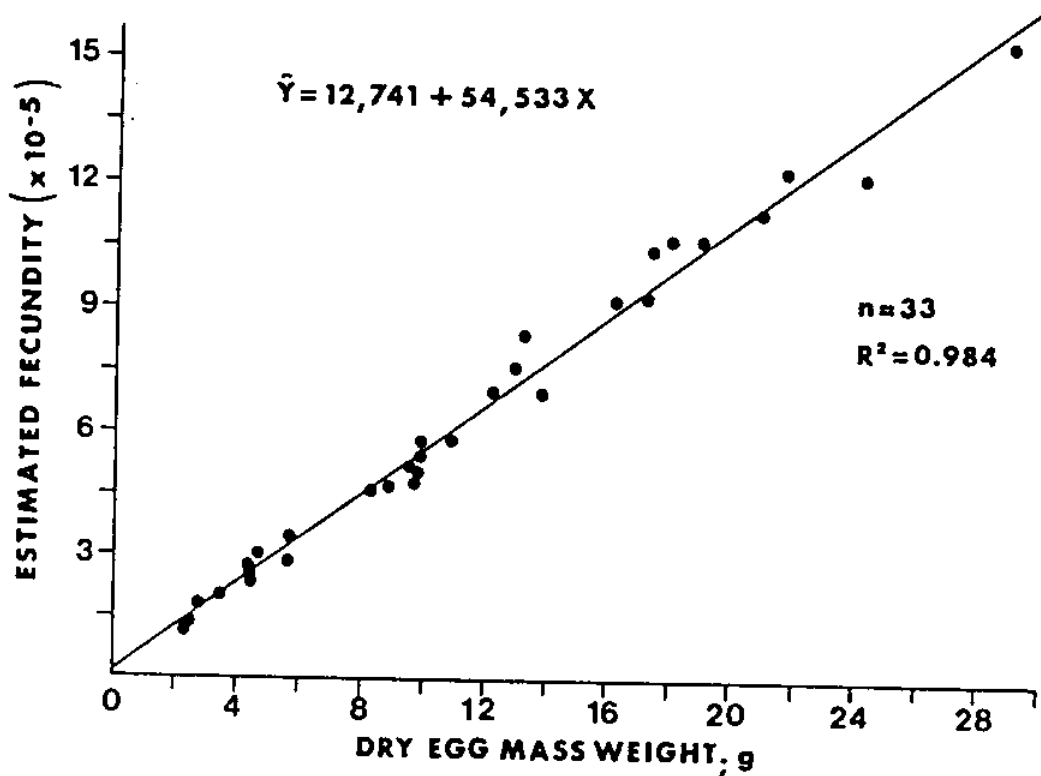$n \approx 33$

$R^2 = 0.984$

Figure 5. Estimated total fecundity, determined by subsampling, plotted against dry egg mass weight for specimens collected during the third project year. Solid line indicates regression line.

Recoveries of tagged ovigerous females revealed that female Dungeness crabs could extrude viable egg masses without having molted during the most recent molting/mating season(s). Of a total of 96 tagged ovigerous crab which were recovered after a single molting season at large, only 25 had molted. Seventeen ovigerous females were recovered after two molting seasons at large and, of these,
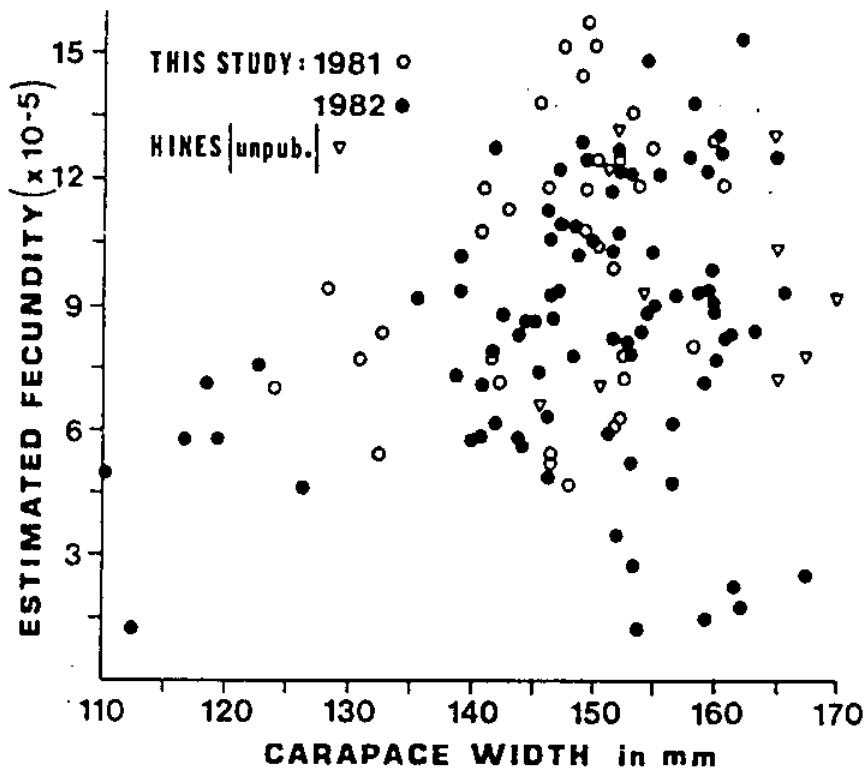
Figure 6. Estimated total fecundity plotted against carapace width for specimens collected during the second (1981) and third (1982) project years and for ten specimens collected off the Farallone Islands, California (courtesy of A. Hines, pers. comm.)

none had molted twice and three had failed to molt for two consecutive seasons. Tag recovery data thus conclusively showed that annual molting and mating were not required to allow female Dungeness crabs to extrude viable egg masses.

That female crabs could extrude viable egg masses in the absence of molting suggested to us that at least part of the apparent variation in size-specific fecundity might be attributed to molting history. When used as a categorical or dummy variable in a multiple regression context, the addition of molting history increased the amount of explained variation in fecundity from about 6% (carapace width alone) to about 30% (carapace width and molting history). For crabs which had molted during the most recent molting season, total fecundity significantly increased with carapace width. For crabs which had failed to molt in the most recent (and perhaps previous) molting season(s), total fecundity significantly decreased with carapace width. Using the "extra" sums of squares principle" (Draper and Smith 1981), we found that the regression line for the molted group was significantly different from the regression line for the group that had failed to molt, but not from the regression line for the uncertain group. The regression line for the group that had failed to molt was significantly different from both the molted and uncertain groups' regression lines (Figure 7). Details of these analyses will be presented in Hankin and Ianelli (in prep.).
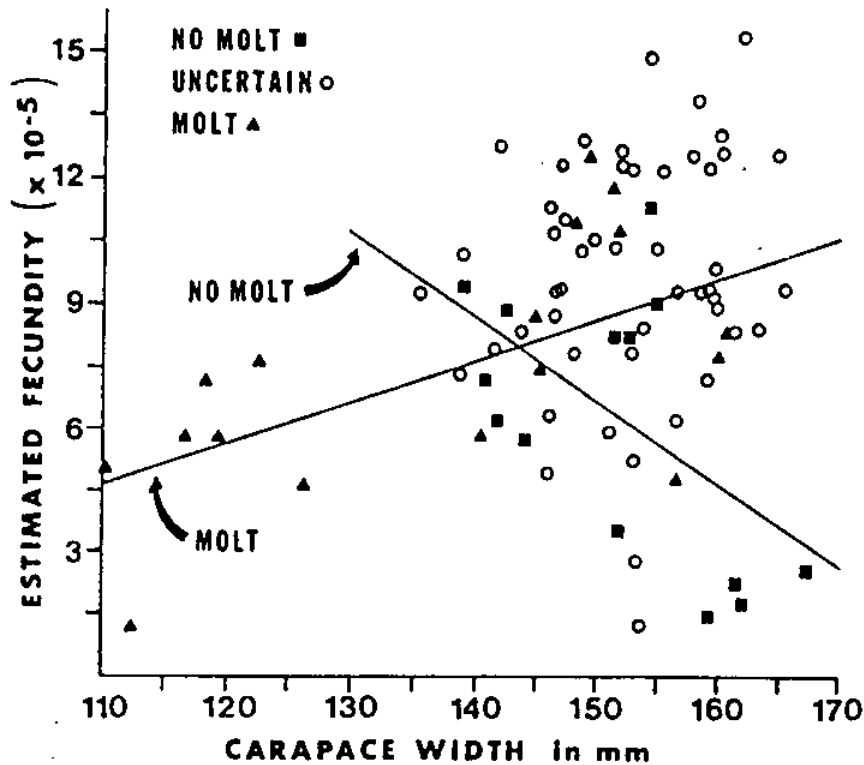
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Figure 7. Estimated total fecundities for crabs which had failed to molt during most recent molting season(s) (NO MOLT), had molted during most recent molting season (MOLT), or had uncertain molting history (UNCERTAIN) plotted against carapace width. Solid lines indicate regression lines for MOLT and NO MOLT groups respectively.

Survival rates.

Because annual molting probabilities for large adult female crabs were effectively zero, and because crabs of this size were fully vul-nerable to the commercial recovery gear, it was possible to use methods presented in Brownie et al. (1978) and Youngs and Robson (1975) to estimate annual survival rates for these crabs based on the sequence of recoveries for each of the three year's releases. Table 5 displays the recovery matrix used for these estimates; the matrix consists of recoveries of crabs which were recovered within 365 day "years" of the original dates of release (as suggested by W.D. Youngs, pers. comm.). Estimated annual natural mortality rates (M) were, on an instantaneous basis, 1.984 and 2.533 for the first and second years' releases, giving annual natural survival rates of 0.1375 and 0.0794 respectively. Confidence intervals for these two survival rate estimates overlapped, thus indicating that estimated survival rates did not differ significantly between years.

The contrast in recovery pattern between large and small females was striking. Table 6 shows an analogous recovery matrix for crabs released at sizes between 125 and 140 mm. In contrast to Table 5, there are significant numbers of these smaller crabs that were re-covered in the third year after tagging. If one assumes that all crabs of this smaller size range (a) molted into fully vulnerable sizes ($\geq$ 155 mm) by the third year at large, (b) had the same annual survival

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Table 5. Number of crabs ≥ 155 mm carapace width released in each project year and number of these crabs recovered during 365 day "year" periods following date of release.

Year Released	Number Released	Year Recovered			
		1	2	3	4
1981	518	47	9	0	0
1982	384		58	2	0
1983	465			34	8

Table 6. Number of crabs with carapace widths ≥ 125 mm but ≤ 140 mm which were released in each project year, and number of these crabs recovered during 365 day "year" periods following date of release.

Year Released	Number Released	Year Recovered			
		1	2	3	4
1981	1725	30	19	13	0
1982	1922		26	13	5
1983	464			8	4

rates as did the large crabs, and (c) no tags were lost during molts, then there were nearly ten times as many small crabs recovered in their third year at large (from those released during 1981) than would have been expected based on these assumptions (13 vs. 1.39). A conclusion that smaller adult female crabs have much higher annual survaival rates than large adult females is inescapable. An annual natural survival rate of about 50% appears compatible with recovery data for these smaller females. It is worth noting that Reilly and Saila (1978) found that survival rates for C. irroratus females were 5-10% during the last two years of life, but were 40-45% for younger females; Lawton (this Symposium) suggests that C. magister and C. irroratus may be closely related in an ecological sense.

Discussion

The results presented in this paper have allowed us to develop a fascinating and unexpected description of the life history of adult female Dungeness crabs. Of the generated project results, only the finding that molt increments declined linearly with increasing carapace width was expected. Other project results caused us to radically revise our original preconceptions concerning the basic life history of female crabs. Below we give what we feel is a description of the female's life history which is consistent with our project results.

The relationship between the age of a female Dungeness crab and carapace width is clearly a complex one. The rapid decline in annual molting probabilities from about 135 mm through 155 mm, to zero beyond 155 mm, means that the correlation between age and carapace width becomes progressively weaker as females reach sizes exceeding 135 mm. Using the molt increment regression presented in this paper (Figure 2) and an average carapace width two years after settling of 110 mm, it appears that almost all females reach a carapace width of

about 128 mm at three years of age (molt increments for crabs of 110 mm average about 18 mm and annual molting probabilities for a 110 mm premolt size appear close to one). At a carapace width of 128 mm, molt increments are about 15 mm and molting probabilities are still nearly one, so that the majority of females probably reach a carapace width of about 143 mm at age four. Beyond age four, females belonging to a single year class may have many possible (modal) sizes depending on succeeding molt history. A size of 155 mm could be reached as early as age five if a female molted from age four to age five. In contrast, a six year old female could conceivably still be the size of an "average" four year old female; assuming that successive molts are independent of one another and that annual molting probabilities for a premolt size of 143 mm are about 0.5, the probability that a six year old female would have the same size as a four year old female is about $(1-0.5) \times (1-0.5) = 0.25$. An "average" female crab probably molts annually from age three to age four but then takes two years to reach a size of about 156 mm at age six. Having reached this size, annual survival rates are very low (about 10%) implying that maximum longevity is probably not much more than 7 or 8 years of age. Mohr (unpublished) has been developing a crustacean growth model which incorporates both size-specific molting probabilities and size-specific variation in molt increments; this model should provide a far better description of the age and growth relation for female Dungeness crabs than the above crude computations. Nevertheless, the absence of a strong correlation between age and size of females means that length frequency data for female Dungeness crabs are extremely difficult to interpret. Diamond (1983) used sophisticated distribution separation methods to extract size structure from carapace width frequency data collected over the three project years, but we have not presented results of those analyses here; their interpretation is by no means straightforward.

The strong size-dependence of annual molting probabilities was unexpected because C. magister and other Cancer crabs mate only while the female is in a soft-shelled condition, immediately after molting (Hartnoll 1969). Butler (1961) first speculated that large female Dungeness crabs may not molt annually (based on observations of carapace condition) and he called our attention to a report by Lehman and Osborn (1970) which gave tag recoveries for female Alaskan Dungeness crabs; their data are entirely consistent with our much larger tag recovery data set. Clearly, many adult female Dungeness crabs do not molt and mate annually. However, recovery of tagged ovigerous crabs that had been at large through two molting seasons without having molted conclusively demonstrated that female crabs must be capable of retaining viable sperm for periods of at least 2.5 years. (The delay from mating in April-May to extrusion and fertlization of eggs in November is about six months in northern California. Hence, failure to molt for two years while still extruding a viable egg mass implies an ability to retain viable sperm for at least 2.5 years beyond an original molting/mating event.) Extrusion of egg masses by females that failed to molt has also been observed in laboratory settings by Wild (pers. comm.), Jamieson (pers. comm.) and in this study. More remarkable still is the laboratory observation by Wild (pers. comm.) that females can molt without mating and still produce viable egg masses, although these egg masses appear to be smaller than "normal".

It is possible that size-dependent declines in annual molting probabili-

ties and sperm retention abilities are a fairly general feature of the reproductive biology of Cancer crabs; they are certainly not unique to C. magister. Declines in annual molting probabilities with increasing size have been documented for the European edible crab, C. pagurus, (Bennett 1974; Hancock and Edwards 1967; Hancock 1965) and for the East Coast rock crab, C. irroratus (Haefner and Van Engel 1975; Reilly and Saila 1978). Hancock (1965) noted the ability of C. pagurus females to retain sperm for long periods and to extrude viable egg masses in the absence of molting and mating. It seems likely, in fact, that the ability to retain viable sperm for long periods of time and to extrude viable egg masses in the absence of molting and mating is an evolutionary adaptation to the observed declines in annual molting probabilities as adult female crab size increases. Declines in molting probabilities are themselves probably a reflection of energetic constraints. As female crabs become larger, the energetic expense of reproduction apparently becomes large enough to eventually prevent the additional energetic expense of growth via molting; the advantages of large size and increased fecundity apparently conflict with the advantages of repeated reproduction at a smaller size. Although repeated reproduction appears to dominate this "conflict", there are obvious tradeoffs which result. Female Dungeness crabs that extruded egg masses without having molted carried significantly fewer eggs (at a given size) than did females that had molted and mated in the most recent molting season (see Figure 7). In fact, total fecundity actually declined with increasing carapace width among those crabs which were visually characterized as having failed to molt for one or more molting seasons or that were known to have failed to molt based on tag recovery data. This apparent statistical decline in fecundity with increasing size may, however, reflect declines in molting probabilities rather than a real size-dependence of fecundity among crabs which have failed to molt. It is likely that many of those females that we characterized as having failed to have molted had in fact failed to molt for two molting seasons rather than just one; this would be especially likely for females with carapace widths in excess of 150 mm. The "uncertain" group probably contained a mixture of crabs which had failed to molt for just a single season and crabs which had molted during the most recent molting season. Because the uncertain group was not statistically different from the group which had molted, but was significantly different from the group which had not molted, it seems most probable that numbers of eggs extruded (at a given size) progressively decrease with number of molts missed. At this point we can only speculate as to the biological basis for such a decline. Progressively fewer sperm or perhaps less viable sperm may remain as a female fertilizes successive broods at extrusion. Alternatively, continuing physical damage to pleopods, which are not regenerated if crabs fail to molt, may phsyically prevent a large female from carrying a "normal" sized egg mass. This issue and the issue of the tradeoff between reproduction and growth both appear to warrant basic study, from physiological and life history-theoretic perspectives.

Finally, results from this study have led us to the conclusion that adult female crabs become senescent. The decline in molting probabilities with increasing size, the decline in egg numbers among those crabs that failed to molt, and the very low annual survival rates (10%) for large female crabs are all entirely consistent with an hypothesis of senescence and all likely have a physiological basis. One cannot help but be awed by the volume of a Dungeness crab's egg mass as

compared to total body volume. How long can an animal continue to make this kind of reproductive investment? Apparently, female Dungeness crabs can make such a continued reproductive investment only with diminishing success and with dramatic reduction in survival rates. And, there are other bits of evidence, some rather anecdotal, which suggest senescence. The largest female Dungeness crabs in northern California are not handsome animals; they are heavily fouled and present a dramatic visual contrast with relatively clean large males and smaller females (see also Butler 1961). The egg masses produced by these large females are often not only small, but they also look "poor", hard as it is to judge such a vague notion. Meat yields from large females are highly variable and are often lower in percentage than for smaller females (Hankin, unpublished). Furthermore, large females are lethargic animals when compared to their smaller counterparts.

Ironically, we would not have been able to develop this scenario of senescence were it not for fishery management policies that prohibit commercial harvest of female Dungeness crabs. If female crabs were harvested, then larger individuals would have been removed from the population by fishing, leaving only smaller females that showed little evidence of senescence. Although prohibition of female harvest has little biological basis, results presented in this paper suggest that the resource of large females is probably small anyway. Survival rates for large females are very low and transition to these sizes (≥ 155 mm) is probably slow due to low annual molting probabilities for crabs of about 140-145 mm. Hence, a fishery targeted on large female Dungeness crab would probably rapidly deplete available females and, over the long term, be very small compared to the existing male fishery. However, it seems unlikely that harvest of such large females would have any significant impacts on recruitment. Most large females will produce small numbers of perhaps "poor" quality eggs, and these females have only one or at most two years to live (survival rates are about 10%). McKelvey et al. (1980) pointed out that harvest of females exceeding some specified carapace width could have the beneficial effect of damping fluctuations in year class strength of Dungeness crabs, if they are caused by density-dependent egg/larval survival. It may indeed be possible to have too many females on spawning grounds. British Columbia allows commercial harvest of females that exceed the size of legal males and fluctuations in the aggregate British Columbia landings are noticeably smaller than those for other areas (see Hankin, this Symposium). It may be worth considering the possibility that limited commercial harvest of female Dungeness crabs has contributed to the relative stability of Dungeness crab landings in British Columbia.

Acknowledgements

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