Issues Dividing the Crab Work Group

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The issues presented by the crab work group to the Crab Plan Team in September 2005 and SSC in October 2005 belong to two categories, estimating effective spawning biomass and stock-recruitment relationships, and another issue, natural mortality, is worthwhile to discuss.

Issues

How to estimate effective spawning biomass

A. Measure of spawning biomass

This is the spawning biomass that will be considered for the stock-recruitment relationship, so it is an index for crab larval abundance. Because mature biomass is more closely related to larval abundance than is mature abundance, only those measures using mature biomass are proposed. Available options are (i) total mature female biomass, (ii) total male and female mature biomass, (iii) fully mated (effective) mature female biomass, (iv) fully mated mature female and effective mature male biomass, and (v) total mature male biomass. The work group has narrowed the options down to iii and iv. My argument in favor of option iii is that since larvae come from fully mated mature females, effective mature female biomass is a better measure of larval abundance than total effective male and female mature biomass. Mature males are used to derive effective female mature biomass, so effective mature female biomass is also an index for both male and female spawning biomass. Other concerns for option iv are that mature males are used twice, primiparous and multiparous females mate at different times (some males can mate with both groups, and some males may mate with only one group), and a snow and Tanner crab male weighs much heavier than a female, which means one assumes that besides mating and fertilizing eggs, a male plays a much more important role than a fully mated female to produce larvae. The argument for option iv is that it may produce a lower optimal harvest rate than option iii. **So, the debate here is to choose a best biological index (option iii) or an index that may have a lower harvest rate (option iv).**

One argument against option iii is that assumed mating ratio may not reflect complex crab reproductive biology. However, this argument can be used against option iv too. If the assumed mating ratio is not good, we should use option ii, total mature biomass.

Another argument in the work group against option iii is that it is less sensitive to fishing than some other options. That is exactly the foundation of the current crab harvest strategies: protecting females from fishing and only harvesting very large-sized males so that mature males can mate at least once before being allowed to be retained in a fishery. Without size limit and female exclusion, option iii would be very sensitive to fishing.

The extreme insensitivity of option iii to fishing for snow crab is also caused by some questionable parameter values estimated by the model. Among them are growth increments per molt for males, growth difference between males and females, and fishery selectivities for "oldshell" males. The model-estimated growth for males is greater than any values from other studies worldwide (Ito 1970, Kon 1980, Moriyasu et al. 1987, Robichaud et al. 1989, Sainte-Marie et al. 1995, Comeau et al. 1998, & unpublished data by Drs. Otto and Rugolo). This "fast" growth makes males "mature" much earlier than under the normal growth, thus resulting in much more "mature" males for mating. In contrast to the model results, most studies also indicate that immature females <51 mm grow at a similar or faster rate than males with the same size (Ito 1970, Kon 1980, Robichaud et al. 1989). Growth increment per molt is probably the most confounding parameter in a length-based model, is difficult to estimate in the model, and therefore should not be estimated in the model. The current snow crab model also has a hidden assumption that experienced NMFS biologists greatly misclassified shell conditions during the summer survey whereas ADF&G technicians and observers can classify very well when sampling the catch. This inconsistent assumption results in estimates of proportions of oldshell males several times higher in the model than the survey data and greatly underestimates fishery selectivities for "oldshell" males, which in fact are mainly classified as "newshell" during the survey. This underestimation artificially protects many mature males from fishing and increases mature male abundance for mating.

The extreme insensitivity of snow crab effective female spawning biomass to fishing shown in Fig. 3 of Jack and Lou's issue draft report is also caused in part by their application of mating ratio separately to primiparous and multiparous females, which contradicts with the work group consensus that all mature female crab (primiparous and multiparous) are put together for effective female spawning biomass calculation for snow crab.

B. Formulation of effective male spawning biomass

This is required only if a total effective spawning biomass calculation is needed.

The options are (i) using total matable male mature biomass as effective male spawning biomass and (ii) using the biomass of those mature males that are required to fully mate with mature females as effective male spawning biomass. If some mature males are not considered in the calculation of effective female

spawning biomass, then they should not be considered for the effective mature male biomass calculation. **So this is an issue of consistency: option i is not consistent. Note that two work group members who raised this issue and preferred option i also took a position on issue C such that options i and ii are identical. Therefore, it is a non-issue for these two members.**

C. Mating ratio in effective spawning biomass calculation

Male to female mating ratio is used to determine the effective female spawners for spawning biomass calculation.

Mating of crabs is complex and its success depends on the distribution, sex ratio, and size difference between mature female and male crabs. In confined environments, large male red king crab (>140 mm CL) in Kodiak are capable of mating with 7 to 9 female crab successfully (Powell et al. 1974), and sublegal males can breed successfully with an average of five females (Powell and Nickerson 1965). Another laboratory study also shows that most male red king crab ≥140 mm CL can fertilize at least three females during the brief period when most multiparous females breed (Paul and Paul 1997). Small red king crab males (120-139 mm CL) are generally successful at fully fertilizing egg clutches of at least 2 to 4 females, and male red king crab >90 mm CL can generally fertilize at least one female in a laboratory (Paul and Paul 1990). A mature male Tanner crab can mate with a maximum of 8-10 females in a laboratory setting during a breeding season (Paul 1984).

Female Tanner and snow crab can store sperm for more than 1 year. Stored sperm from the first mating cannot fertilize the second year's clutch for Tanner crab (Paul and Paul 1992); however, stored sperm from multiple matings may fertilize the subsequent 2 years' clutches (Paul 1984). In a laboratory setting, sperm stored at the first mating (either by adolescent and adult males) is effective for fertilizing the second clutch in snow crab (Sainte-Marie and Carriere 1995). The work group does not consider sperm storage and assumes females need annual mating for fertilization.

Male snow crab are sperm conservers, partitioning sperm among successive matings, and female snow crab are polyandrous (Urbani et al. 1998, Rondeau and Sainte-Marie 2001). Both mate-guarding time by males and the quantity of ejaculate stored in a primiparous female's spermatheca were positively related to the sex ratio of males to females, but these relationships may change over time (Rondeau and Sainte-Marie 2001). Therefore, lack of males for mating may rarely occur for snow crab, but sperm limitation can occur naturally if males allocate their sperm too parsimoniously among females (Rondeau and Sainte-Marie 2001). Because of this sperm economy, it is difficult to use sex ratio to determine effective spawning biomass. Furthermore, depending on temperature, embryo development of snow crab can take 1 or 2 years (Sainte-Marie 1993, Moriyasu and Lanteigne 1998), further complicating the methods used to

estimate effective spawning biomass. Because of the complex reproductive biology of snow crab, Zheng and Kruse (2003) defined effective spawning biomass as the sum of total biomass of mature females, oldshell mature males and 30% of newshell mature males for EBS snow crab.

Based on the above literature review, it is difficult to find a single mating ratio to reflect the complex mating biology. Several studies tried to use multiple ratios to estimate effective spawning biomass. Zheng et al. (1995a) assumed mating ratios from 1:1 to 1:3 based on the CL of a mature male with both newshell and oldshell males participating in mating for Bristol Bay red king crab. Zheng and Kruse (1998) assumed that a male Tanner crab could mate, on average, with a maximum of 5 primiparous females and 3 multiparous females at high density and 1 primiparous and 1 multiparous female at low density. Siddeek et al. (2004) assumed that a pre-recruit snow crab male can mate with 4 primiparous or 3 multiparous females and that a recruit and post-recruit snow crab male can mate with up to 9 primiparous or 6 multiparous females.

Sex ratios of mature crabs may provide some information for selecting a range of mating ratios although errors on shell age classification may limit their usefulness. Sex ratios changed greatly from 1972 to 2004 for Bristol Bay red king crab, with a mean of 1:9.3 (males:females) and a median of 1:6.1 excluding newshell males (Fig. 1a). The mean is 1:1.7 and the median is 1:1.5 when using both newshell and oldshell males to compute sex ratios. Under the assumption that only oldshell males can mate, a mating ratio of 1:3 means that less than 50% of mature females get fully mated in half of the years during 1972-2004 for Bristol Bay red king crab. A mating ratio of 1:2 results in only 33% of mature females fully participating in reproduction in half of the years. Mean clutch fullness for newshell females during this period was about 87% (Fig. 1b). It is not clear what percentage of egg clutches were fertilized. In 1997, 2004 and 2005, due to relatively good recruitment and earlier maturity of females than males, the sex ratios of oldshell mature males to mature females were 1:7.6, 1:7.1, and 1:8.2 (Fig. 1a), and the corresponding egg clutch fullness were 87.3%, 86.4%, and 80.6% (Fig. 1b). If red king crab females need to be mated for extruding egg clutches (see Appendix B) and only oldshell males can mate, mating ratios must be very high (up to 1:8) to produce these egg clutches.

Sex ratios for snow crab over time (Fig. 2) were even more variable than those for red king crab. With oldshell males, the median sex ratio from 1978 to 2004 is 1:26.7 (males:females) from area-swept estimates, 1:7.13 from Jack's model estimates made in 2004, and 1:3.8 from the model estimates made in 2005. Because mature females have lower survey catchability than mature males due to smaller sizes, sex ratios from area-swept estimates should be lower than the true values if shell conditions are classified correctly. The model estimates of oldshell mature males may be 3 to 8 times higher than the area-swept estimates. The sex ratios with only oldshell males by the model are similar to or lower than the sex ratios with both newshell and oldshell males from area-swept estimates.

High estimates of oldshell mature males by the model are probably due to low assumed natural mortality and low estimated fishery selectivities for oldshell males. With sharp differences between model estimates in 2004 and 2005, it is not clear if the model is ready to provide results for management. Even with the low sex ratios from the model, a 1:3 mating ratio results in model estimates of only 42% of mature females fully participating in reproduction in half of the years during 1978-2004 with the 2004 assessment and 79% with the 2005 assessment. These percentages are 24% and 45%, respectively with the 2004 and 2005 model assessments with a mating ratio of 1:1.7. The average egg clutch fullness estimated from the survey from 1975 to 2005 is 79% for newshell females, 76% for oldshell females, and 49% for very oldshell females.

The issue here is how conservative we should be. Should we ignore laboratory results and egg clutch fullness data and assume that every male is needed for fully mating with females even without any fishing, or should we start with a conservative ratio, say 1:3, and examine the impacts to the results? The conservative measures already adopted by the work group include ignoring sperm storage and biennial spawning (in terms of need of males for mating). Alternatively, due to complex reproductive biology for Tanner and snow crabs, it may be wise to ignore mating ratio and use total mature biomass for Tanner and snow crabs.

D. Application of mating ratio in the effective spawning biomass calculation

How should we use the mating ratio to calculate the effective spawning biomass?

Somerton (1981) speculated, based on anecdotal information that bipartite breeding occurs for Tanner crab. In bipartite breeding, pubescent (primiparous) and multiparous females are separated by distance and depth and mated by different sizes of males. Stevens et al. (1993) observed this phenomenon with Kodiak Tanner crab. Bipartite breeding is also reported for snow crab in the Gulf of Saint-Lawrence: Pubescent females were mated in the shallows, mainly by small mature males, and multiparous females were probably mated in deeper waters by large males (Sainte-Marie and Hazel 1992). Therefore, for Tanner and snow crabs, it is reasonable to lump all mature female crabs (primiparous and multiparous) together for effective female spawning biomass calculation, despite different mating times for primiparous and multiparous females for both Tanner and snow crabs and despite having few oldshell mature males in the areas with primiparous females for snow crab.

The disagreement within the work group is whether this bipartite breeding also occurs for red king crab. For the Bristol Bay survey data, which are collected right after the mating of multiparous females, multiparous females occurred more in the southern Bristol Bay than primiparous females during 1974-1977, but they mixed well during 1972-1973 and after 1977 (Fig. 3 & 4). For a

large majority of years, a mature male can spatially mate with both primiparous and multiparous females. Further more, due to different molting times, some red king crab males can mate only with primiparous females, some males can mate only with multiparous females, and maybe some males can mate with both (see Appendix A). Separating primiparous and multiparous females for effective spawning biomass calculation would better address these situations.

E. Time-course of annual events

Molting and mating timings were hotly debated in the work group and now it appears that the group agrees to my suggestion: the mid-point of mating times is set on Feb. 15 for primiparous females and May 1 for multiparous females. The mid-point for molting of juvenile crabs and males is set on April 1. The molting and mating times change each year, and these mid-points are an approximation.

The timing of molting and mating for Bristol Bay red king crab is clear, so no explanation is needed here. For snow crab, they are derived below. From Rugolo and Pengilly's snow crab data (Table 11 of Rugolo et al. 2005), all primiparous females (except 1) have eyed eggs in the January sample; and 53% uneyed eggs, 46% eyed eggs and 1% empty egg case in the March sample. So molting and mating of primiparous females may be primarily in February and March. In the March sample processed during April 14th-May 5th, multiparous females have 76% eyed eggs and 24% uneyed eggs. So, many multiparous females have not hatched and mated during April 14th-May 5th. In the cold water sample in July, about 10% of the multiparous females have eyed eggs. In the snow crab bycatch data, there are females with eyed eggs in May and June, and the survey data seem always to have some females with eyed eggs during June and July. A lab study shows that snow crab hatch during April and May with 0 to 1^0C (Shirley et al. 2005). In summary, hatching and mating of multiparous females may be primarily during March-June with a peak about in April-May, about 2 months later than primiparous females.

It is a little unclear what time males molt to maturity. Rugolo and Pengilly's snow crab data indicate some males molt before March sampling (Rugolo et al. 2005). From summer survey data, males are primarily newshell or oldshell, with a very small proportion being softshell. Based on UW radiometric estimates, softshell males are about 1.5-3 months after molting and older newshell males (shell condition 2+) are about 4 months or longer after molting (Ernst et al. 2005). So males molt primarily during February-May. My interpretation is that males molt to maturity a little earlier than or the same time as the hatching/mating of multiparous females.

This interpretation of these data is consistent with the conclusion of a workshop held in 2001 by a group of Canadian and Alaskan crab scientists, which was that molting and mating of primiparous females peak in February and mating of

multiparous females is 1-3 months later than primiparous females. This interpretation is also in line with the literature for Canadian snow crab. This interpretation and literature all show that the sequence of events of snow crab is similar to that of red king crab although exact times may be a little different.

F. Pre- or post-molt size in female spawning biomass calculation

The issue is whether pre-molt or post-molt carapace size of females should be used to calculate spawning biomass of females.

We should look at this issue based on literature and data. So far, I have not found any data or a published paper that shows that crab fecundity relates only to pre-molt carapace size, not to post-molt carapace size. In fact, all the literature I found relates fecundity to their post-molt carapace size, including the snow crab project report prepared by Rugolo and others (Rugolo et al. 2005). For snow crab, Sainte-Marie (1993) showed that individual eggs of primiparous females are 1.4%-2.7% larger than those of multiparous females but total fecundity of a primiparous female is 16.4%-22.7% less than that of a multiparous female. For Tanner crab, Somerton and Meyers (1983) showed that primiparous females are approximately 70% as fecund as equal-sized multiparous females. However, for the population level, the differences are smaller because some females, primarily multiparous females, with smaller than normal clutch sizes were not included in the snow crab analysis (Sainte-Marie 1993). Although not mentioned in the paper, Somerton and Meyers (1983) might also exclude some multiparous females without eggs or small egg clutches in the analysis because average clutch size in 1981, when sampled in the study, was 82% for newshell females (primiparous females) and 76% for oldshell females (multiparous females) for EBS Tanner crab. Rugolo and Pengilly's snow crab report (Rugolo et al. 2005) shows that fecundity of a primiparous female is generally larger than that of a multiparous female when considering clutch fullness based on the EBS summer trawl survey data (Fig. 5 & 6. Primiparous females are approximated by SC2, and multiparous females are approximated by SC3+, see pages 256-257 of Ernst et al. 2005). Based on these results, we should do nothing or apply at most 20% discount to primiparous Tanner and snow female biomass. Because female red king crab molt each year, estimation of spawning biomass by the two methods do not appreciably change the outcome, but it only complicates the estimation procedure. Because of different growth rates between primiparous and multiparous female red king crab, it is not easy to back-compute pre-molt sizes from post-molt sizes.

If we use pre-molt size to compute mature biomass, based on Jack's snow crab growth model (estimated in 2005), a 48 mm CW female weighing 0.132 lb will be projected back to pre-molt size of 34.0 mm CW weighing 0.048 lb, a 63.6% reduction; a 40 mm CW female weighing 0.077 lb will be projected back to pre-molt size of 26.4 mm CW weighing 0.023 lb, a 70.1% reduction. Data do not exist to show that primiparous females have less than 36% of the fecundity of

equal-sized multiparous females. Even if the fecundity is less for primiparous females than full-clutch multiparous females, the clutch fullness can make up the difference. The average egg clutch fullness from 1975 to 2005 for EBS snow crab is 79% for newshell females (primiparous females), 76% for oldshell females (multiparous females), and 49% for very oldshell females (multiparous females). If biennial spawning occurs, annual fecundity per multiparous female will be much less than annual fecundity per primiparous female.

Some Canadian scientists thought snow crab females may hatch only two broods in a lifetime because of biennial spawning (Sainte-Marie 1993, Comeau et al. 1999), and primiparous females contribute >40% of larvae produced by the population in the northwest Gulf of Saint Lawrence (Sainte-Marie 1993). Ernst et al. (2005) also thought that multiparous females with shell conditions 4 and 5 (at least 2 years after last molt) may have limited reproductive contributions to EBS snow crab owing to mortality and reduced fecundity related to senescence. Using pre-molt size to compute mature female biomass reduces the role of primiparous females to reproduction so much that it is contrary to these findings.

This issue is really a non-issue. Using pre-molt size to compute mature female biomass gets bad estimates of female spawning biomass, confuses the public, increases work load for stock assessment, and introduces additional errors on mature biomass through converting post-molt size to pre-molt size.

G. Only non-molting king crab males can mate?

This issue depends on the king crab molting season for males and on the mating season. Some work group members insist that king crabs cannot molt and mate in the same year. This issue is pretty much addressed with issue E above. The mating season for a red king crab population may last from January to July (Otto et al. 1990), and male red king crab may molt in the spring or late summer (Dr. Stevens, see Appendix B). Combining arguments that only oldshell males and non-molting males can mate, for those males molting in mid- or late summer (after the mating season), only a tiny proportion of mature males (those skipping molt for 2 years) can possibly mate. Under the molting and mating seasons assumed in section E (above), this is not an issue for multiparous females. If one accepts that mature males 10.5 months postmolt can mate and a mature male can mate with both primiparous and multiparous females, it should not be an issue for primiparous females also. **It may be reasonable to expect that males cannot mate 2 or 3 weeks before molting. However, it seems there are no biological data to support that no males can mate 1.5 - 7 months before molting. With a long mating season for a population, I think it is not an issue.**

H. Stock assessment modeling issues.

Whether natural mortality changed or not during the early 1980s for Bristol Bay red king crab divided the work group. So is whether molting probability changed over time for male red king crab. This is a big topic so I would not discuss it in details. My view is that natural mortality in the early 1980s was much higher than other periods and that male molting probability changed from periods to periods (Zheng et al. 1995a, 1995b, Zheng and Kruse 2002, Zheng 2005). My view has been supported by the findings of other researchers (e.g., Balsiger, J.W. 1974, Otto 1986, Reeves 1988, Stevens 1990, Greenberg et al. 1991). Because constant natural mortality and male molting probability do not fit well the survey data before the mid-1980s, I offered to run scenarios for the work group with constant natural mortality and male molting probability with the data after 1984.

There are also concerns with the snow crab model. I discussed briefly in section A on some parameters. Other concerns with the 2004 assessment are that estimated growth matrix is too spread out and that residuals contain too much systematic errors, which affects parameter estimation. Without fitting to survey shell condition data, the 2005 assessment greatly reduced systematic errors but created problems in estimating fishery selectivities by shell condition. The biggest concern with the model is the instability of the model. Estimates of time series of exploitable abundance, recruitment, and full selection fishing mortality from the base model changed greatly from one estimate to another. Estimated pristine recruitment level from the estimated S-R curve in 2005 (3.0 billions of crab) is about twice as much as those estimated in 2004 (1.68 billions of crab). So, the snow crab assessment model seems still in a developmental stage.

I. Shell condition of males in calculation of effective spawning biomass

The issue here is how old is old to qualify for mating.

Two options divide the work group: (i) Oldshell males two years or more postmolt can mate with multiparous females, and oldshell males one year or more postmolt can mate with primiparous females; and (ii) males need at least 10.5 months postmolt to mate with primiparous females and 13 months postmolt to mate with multiparous females (or males that molt this spring can mate next spring). Both options are conservative choices, and one is more conservative than the other.

Shell condition at the breeding season depends on the time of the molting season. The molting and mating timings are discussed in section E above.

It is well known that shell conditions affect mating. For Tanner crab, recently molted males do not mate for at least 99 d after molting, and oldshell males

dominate matings contested by newshell males (Paul et al. 1995). Stevens et al. (1993) reported that the proportion of oldshell males grasping multiparous females was much higher than that with pubescent partners. Like Tanner crab, large snow crab oldshell mature males also outcompete small newshell males in mating with females (Sainte-Marie et al. 1999).

Based on many published studies, newshell red king crab males can mate, both observed in the field and laboratory. Among 3618 pairs of mating red king crab observed in nature from 1964 to 1984, most mating males are newshell for CL less than 160 mm (Powell et al. 2002, see Appendix A). It has been demonstrated that male red king crab can mate 10 days or two weeks after molting (Powell et al. 1972, Paul and Paul 1990). A fair amount of males observed in mating pairs were newshell less than four months from their last molting (Powell et al. 2002, Appendix A). Otto et al. (1990) reported that the mating season for a red king crab population may last from January to July, so many mature newshell males will have time for their shell to harden enough to mate before or after molt if there are females around them.

Dr. Brad Stevens (See Appendix B) also thinks crabs several months (>4 months?) postmolt have hard shell and can mate. Based on some literature and data, he also thinks that some proportion of mature male red king crab may molt during late summer and fall and that these males will be several months postmolt during a mating season. Dr. Stevens also thinks that for modeling purposes male red king crab that are coded as shell 2 ("newshell") in the survey may participate in mating (See Appendix B).

For Canadian snow crab, many biologists define intermediate shell condition as 8 months to 3 years postmost (Moriyasu and Benhalima 1998, Biron et al. 2000, Rondeau and Sainte-Marie 2001), and this shell condition is commonly seen in mating pairs (Comeau et al. 1998, Sainte-Marie et al. 1999). In an email on Nov. 15, 2005, Dr. Sainte-Marie wrote:

"I offer the following answer based on our laboratory observations and general patterns in the Northwest Atlantic.

All adult males can mate, except the very softest (from time of molt to about a 5-6 weeks after molting), but newly molted males (shell condition, SC, 1) rarely co-occur (in time or in space) with receptive females. Adult males with new hard shells (SC2, from about 6 months to 1.5 years after molting) readily mate but may be competitively excluded from mating by the more aggressive adult males with intermediate or dirty hard shells (SC3 and SC4, respectively), as would be any newly molted male that happened to be in the right time and place.

Assuming that (1) males molt to adulthood in the March-May period (or even a bit later in some areas of the Northwest Atlantic), (2) females undergo their maturity molt from January to March, and (3) mature females release their larvae and are

receptive to mating sometime from the middle of April to the middle of June, then adult males could not potentially mate with virgin (primiparous) females until the next winter (at about 9 months postmolt age) or multiparous females until the next spring (at about 12-13 months postmolt age). Whether or not SC2 males mate will depend on the intensity of competition from more aggressive males, which in turn depends on the operational sex ratio. If there are a lot of females to be mated and SC3 and SC4 males are scarce (naturally or as a result of intense fishing), then SC2 males will get their chance."

So, it is clear that mating depends on competition and option (ii) (mature males about one year postmolt can mate) is a reasonable, conservative assumption.

J. How to choose a stock-recruitment relationship

J.1. S-R relationship.

Stock–recruitment (S–R) relationships have important implications for harvest strategies but are difficult to develop for crab stocks because crabs lack retainable hard body parts to age them and because our lack of sufficient knowledge about complex crab reproductive biology complicates estimating effective spawning biomass. S–R data from Bristol Bay red king crab and Tanner crab suggest a dome-shaped type Ricker curve, whereas S–R data for snow crab suggest very weak density-dependent relationships (Zheng and Kruse 2003). Periodic or quasiperiodic behavior of recruitment is common in many crab stocks (Zheng and Kruse 2000). In the Northwest Atlantic, Sainte-Marie et al. (1996) hypothesized that density-dependent mortality in juvenile nurseries may cause alternating periods of strong and weak recruitment for snow crab. A strong crab cohort may colonize and saturate available nurseries such that settling megalopae from subsequent cohorts are cannibalized by larger immature crab or are forced to use suboptimal habitats, which may lower survival rates (Sainte-Marie et al. 1996). Once the resident cohort achieves sexual maturity, they move offshore to join the reproductive population, thus vacating the nursery areas for recolonization by a subsequent year class. While this hypothesis has not been proven, it is intriguing as it may help to explain the apparent circular S–R pattern for snow crab in the EBS and Northwest Atlantic.

Even though Beverton-Holt type curves do not fit the crab data as well as Ricker type curves, Beverton-Holt curves usually result in lower harvest rates and thus are more conservative than Ricker curves. Therefore, both curves should be examined in overfishing/overfished definitions.

J.2. Steepness parameter (Tau) range for S-R curves: The parameter related to the steepness near the origin of the stock-recruitment curve.

The steepness parameter indicates the productivity of a stock and the optimal harvest is very sensitive to this parameter. A lower Tau value means a higher productivity. Mace (1994) reported that the overall average value of Tau was 0.19, with the 80th percentile of Taus being 0.3, for 83 fish stocks in the Atlantic. She suggested a Tau range of 0.05 to 0.35 (Mace 1994). Clark (1991) used a Tau range of 0.06-0.25 for "a range of realistic spawner-recruit relationships" to estimate exploitation rates for Pacific demersal fish stocks. For a long-lived Pacific fish stock, such as Pacific ocean perch (*Sebastes alutus*) with an assumed natural mortality of 0.05, Clark (2002) used a Tau range of 0.06-0.67. For crab stocks in the EBS, Dr. Siddeek estimated Tau to be 0.17 for Bristol Bay red king crab, 0.09 for Bristol Bay Tanner crab, and 0.08 for EBS snow crab, based on the data up to 2004. **If a Tau value is available, it can be used in simulations. For stocks without estimated Tau values, to be conservative, I suggest using a lower productive Tau range (0.1-0.3) than estimated for simulations to define overfishing/overfished levels for the EBS crab stocks.** A Tau range of 0.4-0.5 is for a long-lived stock with maximum ages of over 40 years.

K. Natural mortality

A variety of approaches have been used to estimate *M* for animal stocks. These approaches range from simple life-history analysis to complex mark-recapture experiments and population modeling. Each has its own data requirements and limitations. Based on literature on 14 crab stocks worldwide, mark-recapture experiments, population models, and life-history analysis are three commonly-used methods for crab stocks (Zheng 2005). The most significant feature of *M* estimates for crab stocks is high variation. Different approaches result in different estimates. With the same estimated maximum age, estimated *M* in the literature appears to be higher for crabs than for fish, and Hoenig's (1983) equation (for all species) results in lower *M* than overall published *M* in the literature for crab stocks (Zheng 2005).

Five published papers have estimated *M* for snow crab:

a. Otto (1998): ranging from *M* = 1.07 to 2.11 with an asymptotical *M* of 1.07 for mature males based on a ratio method.
b. NPFMC (1999): *M* = 0.3 for mature crab based on Hoenig's equation with maximum age of 15.
c. Zheng (2003): *M* = 0.27 to 0.97 with the best estimate of 0.35 for mature males and 0.52 for mature females based on population modeling.
d. Wade et al. (2003): *M* = 0.26 to 0.48 with the best estimate of 0.4 for mature male Atlantic snow crab >94 mm CW based on survey and catch data.

e. Siddeek et al. (2004): *M* = 0.1 to 3.0 based on size, shell condition and sex for Atlantic snow crab (estimated by Dr. B. Sainte-Marie from tag-recapture data), with females having higher *M* than males.

A variety of *M* values have been published in many papers for red king crab, and these mostly range from 0.1 to 1.0 (Zheng 2005). Overall, *M* estimates for females are generally higher than for males. This makes sense because mature females molt each year and are subject to higher predation mortality than mature males (Livingston 1989).

I surveyed the stock assessment reports by ICES, Northeast Fisheries Science Center, Alaska Fisheries Science Center, and Northwest Fisheries Science Center and found out that *M* used for their stock assessments are generally similar to those estimated by Hoenig's equation or higher. Multiple species VPA used by ICES and the Alaska Fisheries Science Center estimated a much higher *M* for juvenile animals than those based on Hoenig's equation (e.g., Livingston and Methot 1998; Hollowed et al. 2000; ICES 2002). Predation on snow and Tanner juvenile crabs by groundfish was also very high in the EBS. Up to 95% and 58% of the reconstructed population numbers of age 1 Tanner and snow crabs were consumed by Pacific cod alone during summer months (Livingston 1989).

Biologically, *M* for crab populations is probably a function of size, shell condition, age, and sex, with a high value for small juveniles due to predation and old animals due to senescence. *M* may increase greatly after certain ages, as estimated by Dr. B. Sainte-Marie from tag-recapture data for Atlantic snow crab (Siddeek et al. 2004). Ernst et al. (2005) suggest "that maximum post-terminal molt lifespan in the EBS is on the order of 6-7 years" based on radiometric methods and tracking of an identifiable pseudo-cohort. Ernst et al. (2005) also cited the radiometric study by Canadian scientists that post-terminal molt snow crab can live a maximum of 5-6 years. Survey data from the EBS show that few mature female snow crab can live more than 4-5 years (Fig. 7). Note that fisheries bycatch of females is very low. However, it is a challenge to get data to estimate such detailed age-based or size-based *M* values.

I suggested a simple, conservative (lower) *M* based on Hoenig's equation (for all species) and estimates of maximum ages of 18 for male snow crab (*M* = 0.25) and 13 for female snow crab (*M* = 0.34) (Siddeek et al. 2004, provided by Dr. B. Sainte-Marie) and maximum age of 22-24 for male red king crab (*M* = 0.2) (NPFMC (1999). *M* for female red king crab is assumed 25% higher than for males (*M* = 0.25). Based on the literature, a higher *M* should be considered for sensitivity studies for snow crab.

Some work group members want a much lower *M* than these. A compromise for the whole work group in 2004 was to assume a maximum age of 20 years for male snow crab, 25 years for red king crab, and to use a 1% rule approach (i.e., only 1% of crabs live to the maximum age from age 0 under natural condition). The result of the compromise is *M* = 0.18 for male red king crab and *M* = 0.23 for male snow crab.

M for females has still not been agreed on. Since juvenile male and female crabs have similar growth rates and mature females have much smaller body sizes than mature males, it is generally believed that female crabs mature earlier than males. Molting to maturity for Tanner and snow crabs is terminal molt, so female Tanner and snow crabs should have lower maximum ages than males, which is reflected in my suggestions above based on Siddeek et al. (2004). Since we use maximum ages to estimate *M* and females have lower maximum ages, females should have a higher *M* than males.

In a reply to Jack on Feb. 3, 2003, Dr. Sainte-Marie wrote his justification for the maximum ages and *M* used in Siddeek et al (2004):

"*As for adult males, the estimates of maximum age after terminal molt are based on a few individuals aged by radiometric methods (Conan and Orensanz have separately reported some values) and on my rather extensive tag-recapture study in the unfished Saguenay Fjord. The maximum ages are probably good figures, although exceptionally some individuals may perhaps live longer. The partitioning of mortality with time after terminal molt is not so certain, but my overall impression is that mortality escalates rapidly in post-terminal molt years 4 and up. Anyway, by year 5 or 6, male physiological condition and appearance deteriorates rapidly and males become less available (and certainly less desirable) to the fishery. I think the Moncton group are working on some natural mortality estimates for adult males; will know more next week when I visit with them.*"

The "overall impression" by Dr. Sainte-Marie about much higher *M* 4 years after mature is also consistent with the survey data in the EBS (Fig. 7).

A lower *M* generally results in more conservative harvest strategies based on yield/spawning biomass per recruit analysis. **The *M*s I suggested are lower than those in the literature and those estimated by the survey and tagging data. The compromised *M*s are even lower. The question is how low is low enough. If *M* is set to be too artificially low, we may generate artificial results in stock assessments and computer simulations.**

Results between Two Choices within the Work Group

Even though there were sometimes different opinions from each of the four work group members, the work group generally divided into two viewpoints or scenarios, as follows.

1. These are my choices, based on the above justification. These choices are basically supported by myself and Dr. Siddeek:
   (1) Measure of spawning biomass: Fully mated (effective) mature female biomass.
   (2) Mating ratio: 1:3.
   (3) Application of mating ratio in the effective spawning biomass calculation: combining primiparous and multiparous females and then applying the mating ratio for both Tanner and snow crabs, and applying the mating ratio separately to primiparous and multiparous females for king crabs.
   (4) Pre- or post-molt size in female spawning biomass calculation: Use post-molt size for both primiparous and multiparous females.
   (5) Shell condition of males in effective spawning biomass calculation: males need at least 10.5 months postmolt to mate with primiparous females and 13 months postmolt to mate with multiparous females.
   (6) S-R relationship: consider both Ricker and B-H
   (7) Steepness parameter (Tau) range for S-R curves: 0.1-0.3.
   (8) M: Two options: (i) 0.18 for king crabs and 0.23 for Tanner and snow crabs; (ii) 0.18 for male king crabs and 0.23 for male Tanner and snow crabs, and 0.22 for female king crabs and 0.29 for female Tanner and snow crabs.

2. The alternative choices, as I understand them:
   (1) Measure of spawning biomass: The sum of total matable mature male biomass and fully mated (effective) mature female biomass.
   (2) Mating ratio: ratio of total mature females/(total mature males of 2 yr oldshell for Tanner and snow crabs and non-molting for king crabs) with F = 0. Or, every mature male is needed for mating under pristine conditions.
   (3) Application of mating ratio in the effective spawning biomass calculation: combining primiparous and multiparous females and then applying mating ratio for king, Tanner and snow crabs at multiparous females' mating time.
   (4) Pre- or post-molt size in female spawning biomass calculation: Use pre-molt size for primiparous females and post-molt size for multiparous females for all crab species.
   (5) Shell condition of males in effective spawning biomass calculation: for Tanner and snow crabs, oldshell males two years postmolt can mate with multiparous females, and oldshell males one year postmolt can mate with primiparous females; for king crabs, mature males at least 10.5 months postmolt and non-molting during the same year can mate.
   (6) S-R relationship: B-H.
   (7) Steepness parameter (Tau) range for S-R curves: 0.1-0.45.
   (8) M: 0.18 for king crabs and 0.23 for Tanner and snow crabs.

(Based on the issue draft report by Jack and Lou on 2/10/2006, their position on two years postmolt has been changed to one year postmolt. So two years postmolt of 2(2) and 2(5) is now replaced by one year postmolt for comparison purpose here).

Dr. Siddeek has analyzed these two scenarios and obtained the results as follow (given the problems with the current snow crab assessment model, only red king crab results are compared in Tables 1 and 2). Mature male harvest rate at survey time is comparable to the mature male harvest rate of the current harvest strategy. With scenario 2, the overfishing mature male harvest rate is about 6% and the target rate is less than 5%. With scenario 1, the overfishing mature male harvest rates are from 16.4% to 18.6%, and the target rate is less than 15%.

Table 1 Estimates of limit reference points for the base input parameter values for Bristol Bay red king crab for different mating ratio and effective spawning biomass calculations for a range of stock-recruitment model steepness parameter (τ) values. The recruits are generated from deterministic Beverton and Holt (BH) and Ricker (RC) stock-recruitment (S-R) models under effective spawning biomass calculated in different ways with an initial sex ratio of 1:1. Handling mortality rate: 20%. Trawl bycatch mortality rate: 80%. ESB= Effective spawning biomass estimated accounting for male to female mating ratio, SSB = Mature biomass estimated without accounting for mating ratio.

Scenario	2	1a	1b
S-R Model (Recruit - ESB)	BH	BH & RC	BH & RC
Effective Spawning Biomass Estimation	Female ESB + Male SSB	Female ESB	Female ESB
Mating Ratio	Estimated at F=0: 1: 2.21	1:3	1:3
τ range	0.1-0.45	0.1-0.3	0.1-0.3
M (male, female)	0.18, 0.18	0.18, 0.18	0.18, 0.22
$F_{x\%}$	56	51	58
F value corresponding to $F_{x\%}$	0.11	0.45	0.57
Legal Harvest Rate at Fishing Time (Oct 15)	0.0905	0.2968	0.3534
Mature Harvest Rate at Survey Time (June 15)	0.0608 (≥120mmCL)	0.1638 (≥120mmCL)	0.1858 (≥120mmCL)
% Mean Mated Females	62	61	68
MSY achieved	78	84	86

A simple approach is to use total mature biomass, regardless of shell conditions and mating ratio. Under this simple approach, (1)-(5) of two scenarios are identical. The results for red king crab with total mature biomass are shown in Table 2 for scenario 1. Interestingly, the results with effective female spawning biomass and total mature biomass are very close for scenario 1.

Table 2. Estimates of limit reference points for the base input parameter values for Bristol Bay red king crab for a range of stock-recruitment model steepness parameter (τ) values. The recruits are generated from deterministic Beverton and Holt (BH) and Ricker (RC) stock-recruitment (S-R) models under total mature biomass calculated in different ways with an initial sex ratio of 1:1. Handling mortality: 20%. Trawl bycatch mortality: 80%. SSB = Total mature biomass estimated without accounting for mating ratio.

Scenario	1a	1b
S-R Model (Recruit - SSB)	BH & RC	BH & RC
τ range	0.1-0.3	0.1-0.3
M (male, female)	0.18, 0.18	0.18, 0.22
$F_{x\%}$	51	49
F value corresponding to $F_{x\%}$	0.55	0.51
Legal Harvest Rate at Fishing Time (Oct 15)	0.3444	0.3259
Mature Harvest Rate at Survey Time (June 15)	0.1824 (≥120mmCL)	0.1754 (≥120mmCL)
MSY achieved	93	91

Spawning biomass per recruit is shown in Fig. 8a for scenario 1 and Fig. 8b for scenario 2 for red king crab.

Model Simplifications/Assumptions

Model simplifications or assumptions could lead to higher (liberal, "+") or lower (conservative, "-") than the true harvest rates. The followings are a partial list of model simplifications/assumption for the crab work group:

(1) No consideration of spatial dynamics (+).
(2) No male/female size difference consideration for snow crab although body sizes of mature males are generally much larger than mature females (+).
(3) No stored sperm for Tanner and snow females (-).
(4) No biennial spawning of female snow crab (in terms of need of males for mating each year) (-).
(5) Extremely low natural mortality (-).
(6) Assuming low productivity (higher Tau values) of S-R curves (-).
(7) No consideration of mating competition for males (or only strong males can mate) (-).
(8) High handling mortality rate for snow crab (-).
(9) Much lower mating ratios than observed in labs (-).

Model simplifications and assumptions are biased toward the conservative side.

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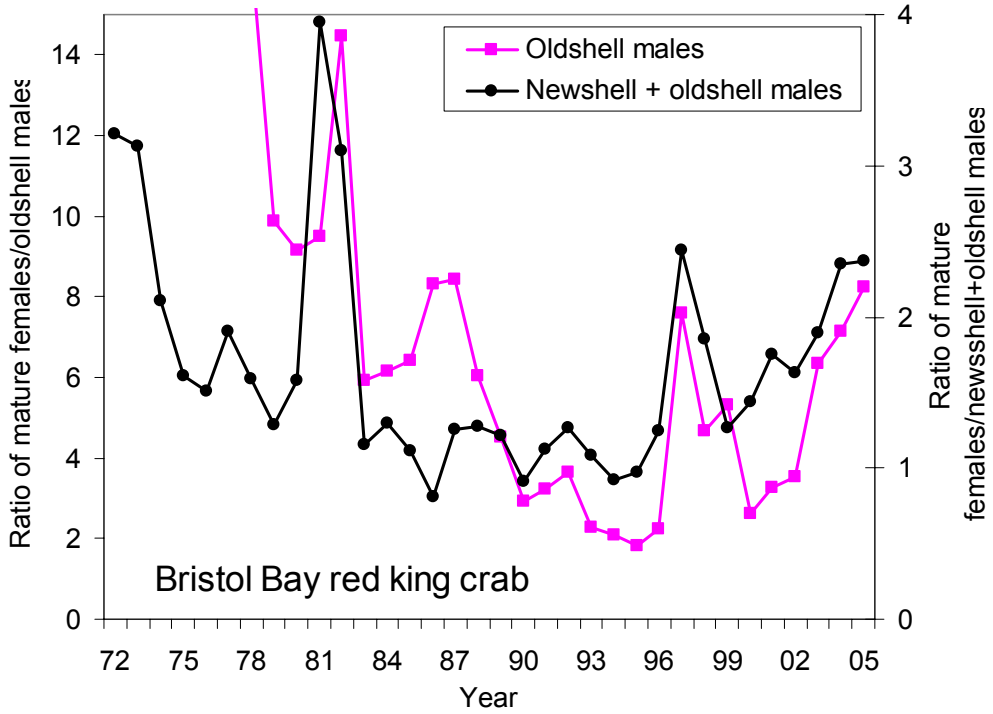

Figure 1a. Ratios of mature females (>89 mm CL) to mature males (>119 mm CL) from 1972 to 2005 from the results of the length based model for Bristol Bay red king crab.

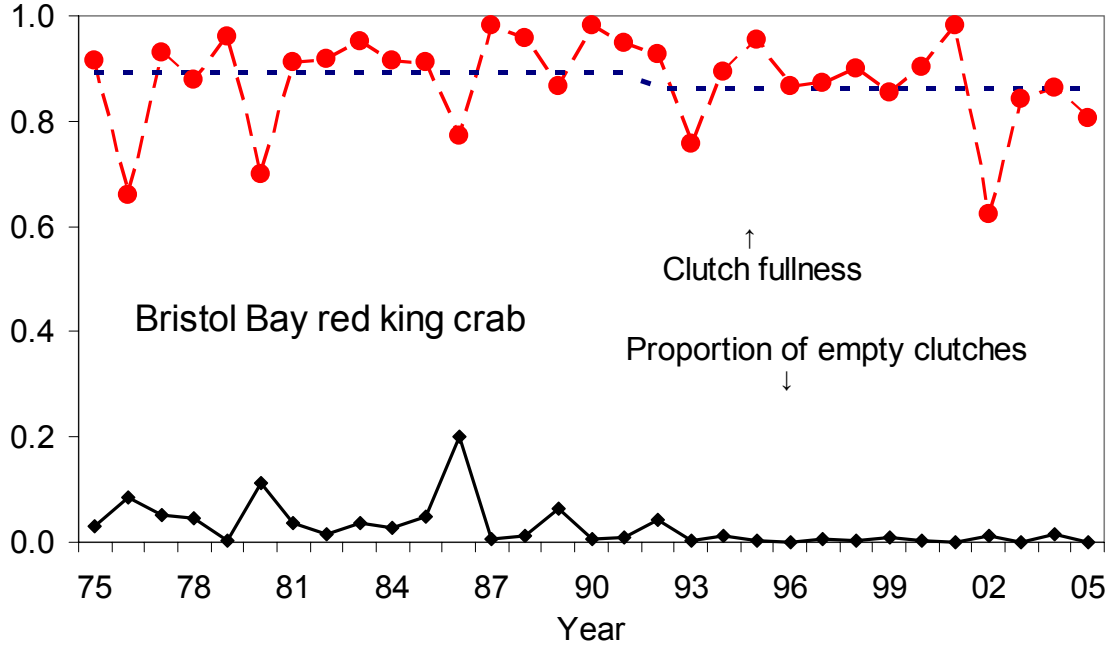

Figure 1b. Average clutch fullness and proportions of empty clutches of newshell (shell conditions 1 & 2) mature female crab from 1975 to 2005 from survey data. Oldshell females were excluded for computation. A scale 0-6 was used to measure clutch fullness. Blue dashed line is the means during two periods.

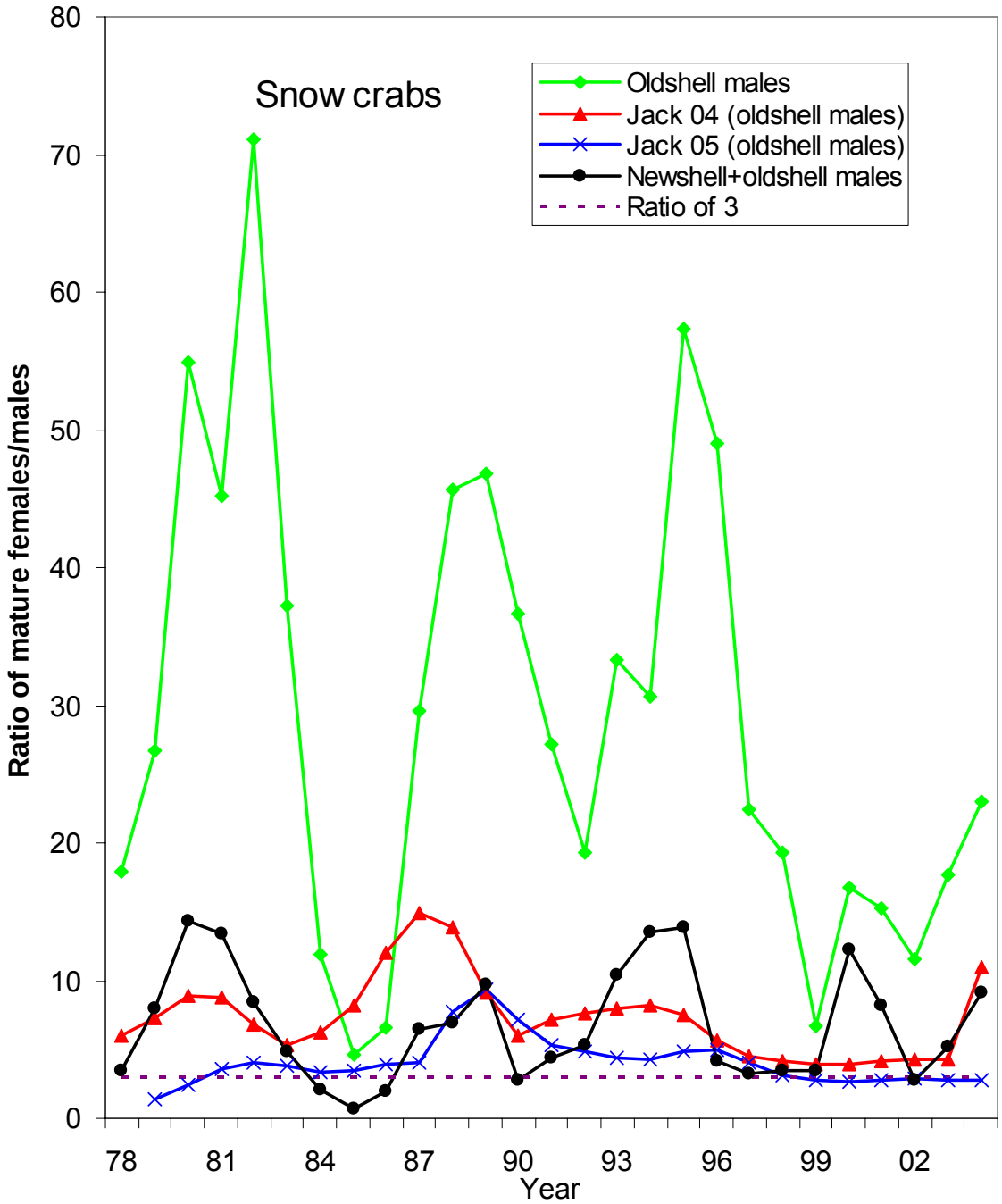

Figure 2. Ratios of mature females to mature males from 1978 to 2004 for eastern Bering Sea snow crab. "Jack 04" and "Jack 05" are results from the population models in 2004 and 2005, and maturity is defined by mature curves. The other two series of sex ratios were computed from the area-swept estimates with maturity of females being determined by morphology during the survey and mature males being >87 mm CW.

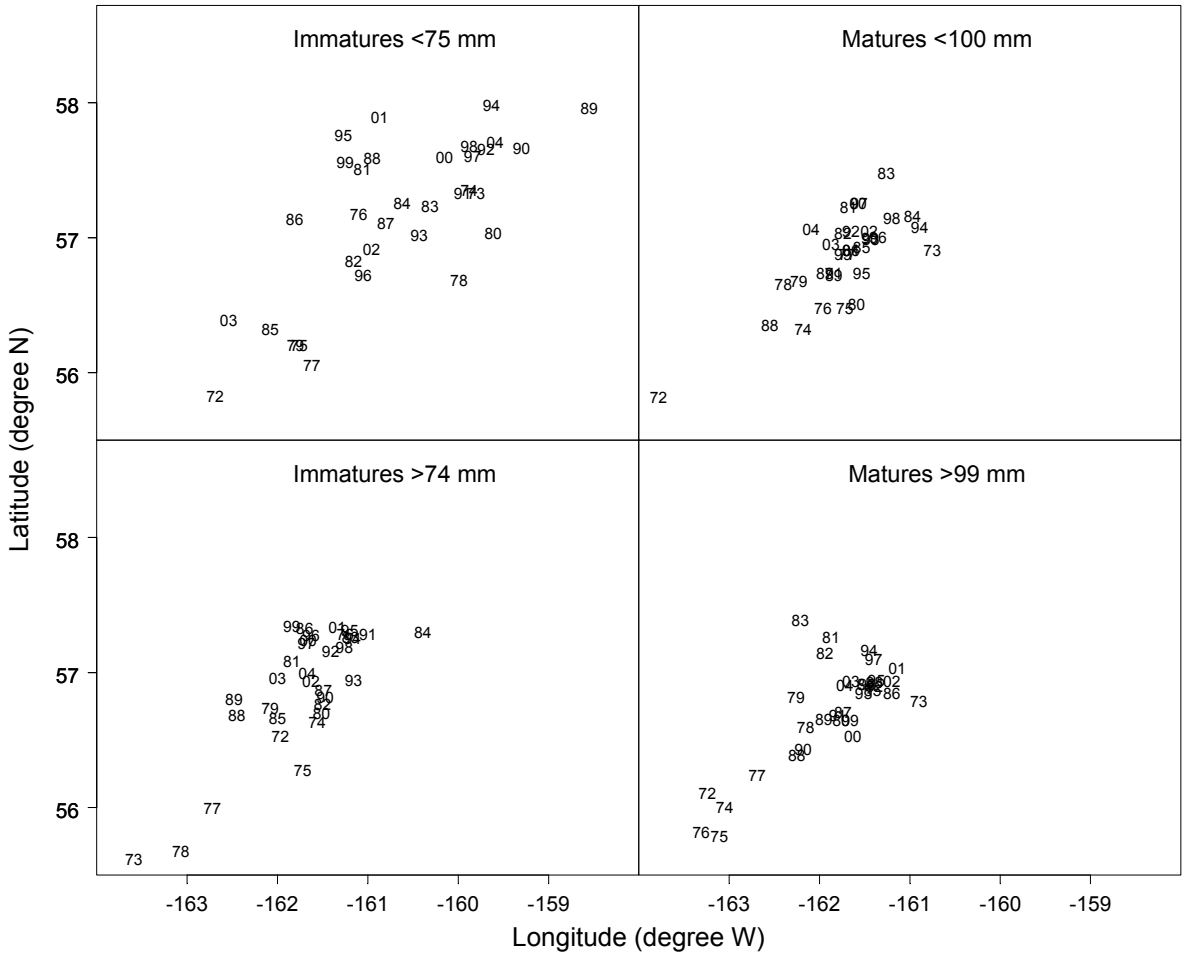

Figure 3. Distribution centers of female abundance for Bristol Bay red king crab. Matures >99 mm CL is an approximation of multiparous females, and matures <100 mm CL is an approximation of primiparous females.

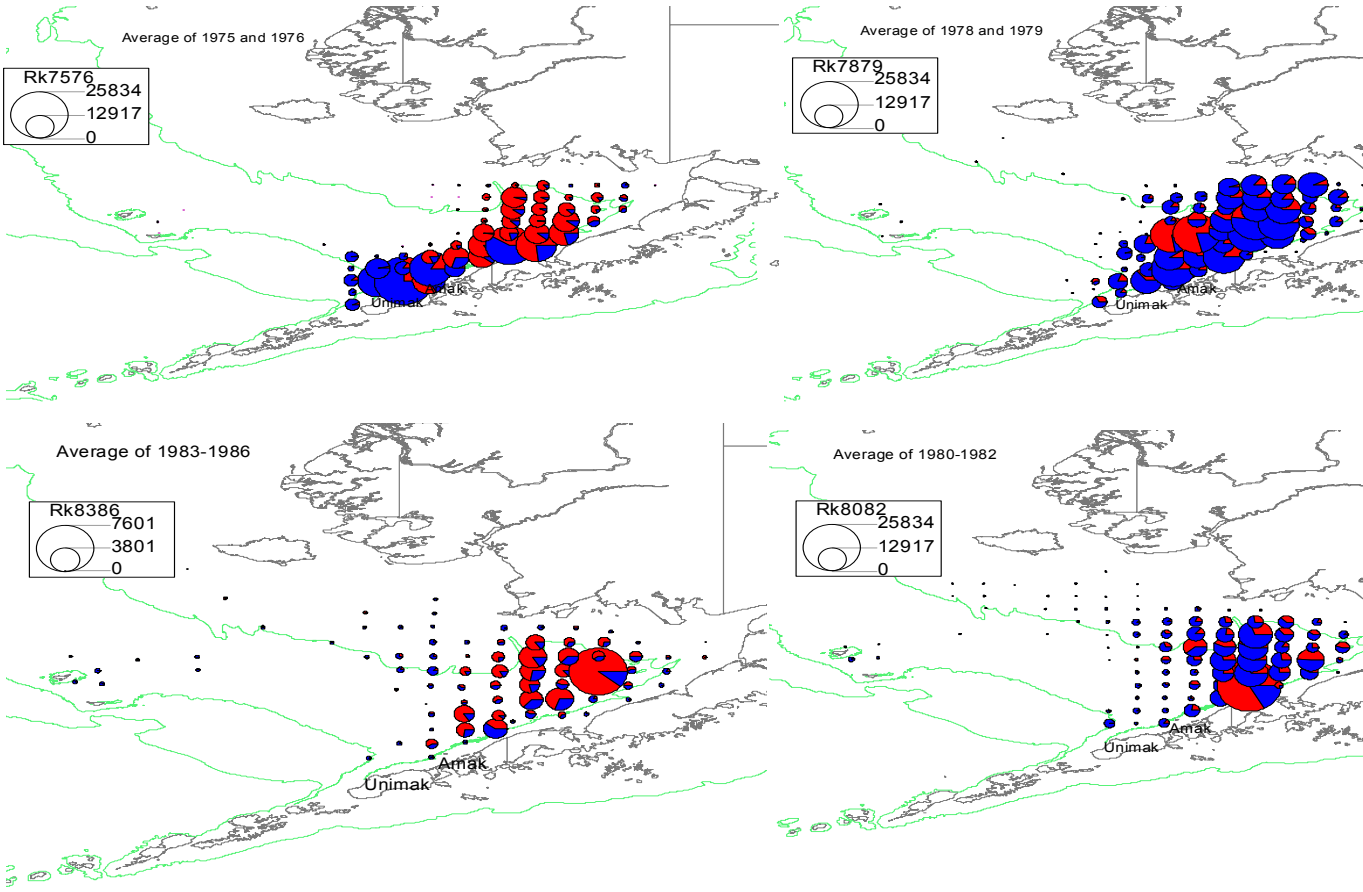

Figure 4. Geographic distributions of mature female red king crab from 1975 to 1986 in the EBS derived from NMFS summer trawl survey data. Red color is for females <100 mm CL (primarily primiparous) and blue color for females >99 mm CL (primarily multiparous). The diameter of each pie represents crab density expressed as the number of crab per square nautical mile. Three depth contour lines are 50, 100, and 200 m.

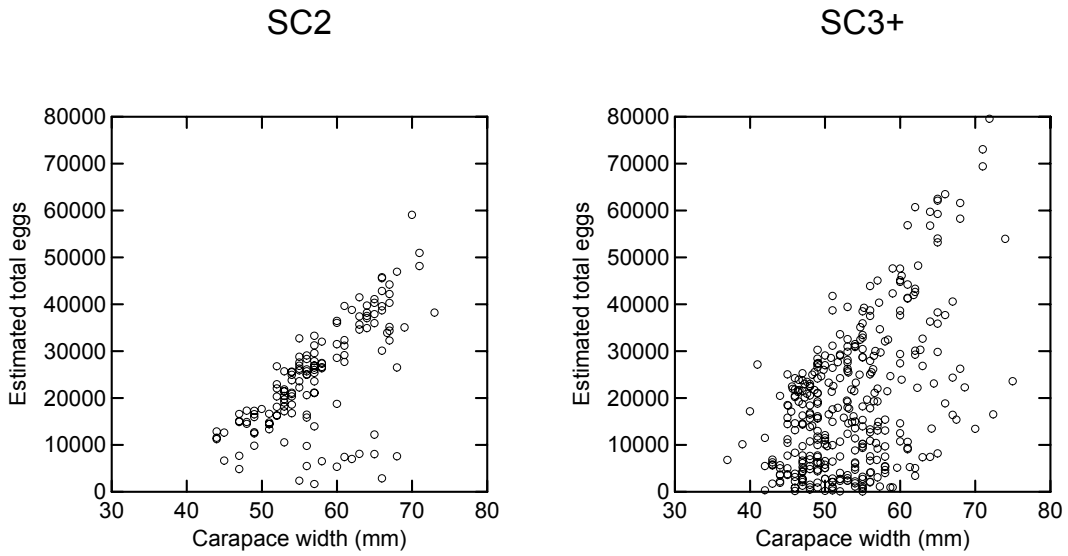

Figure 5. Scatterplots of estimated total eggs per clutch on carapace width for 499 ovigerous Eastern Bering Sea snow crab females grouped by shell condition codes. Primiparous females are approximated by SC2, and multiparous females are approximated by SC3+. (Source: Figure 9 of Rugolo et al. 2005).

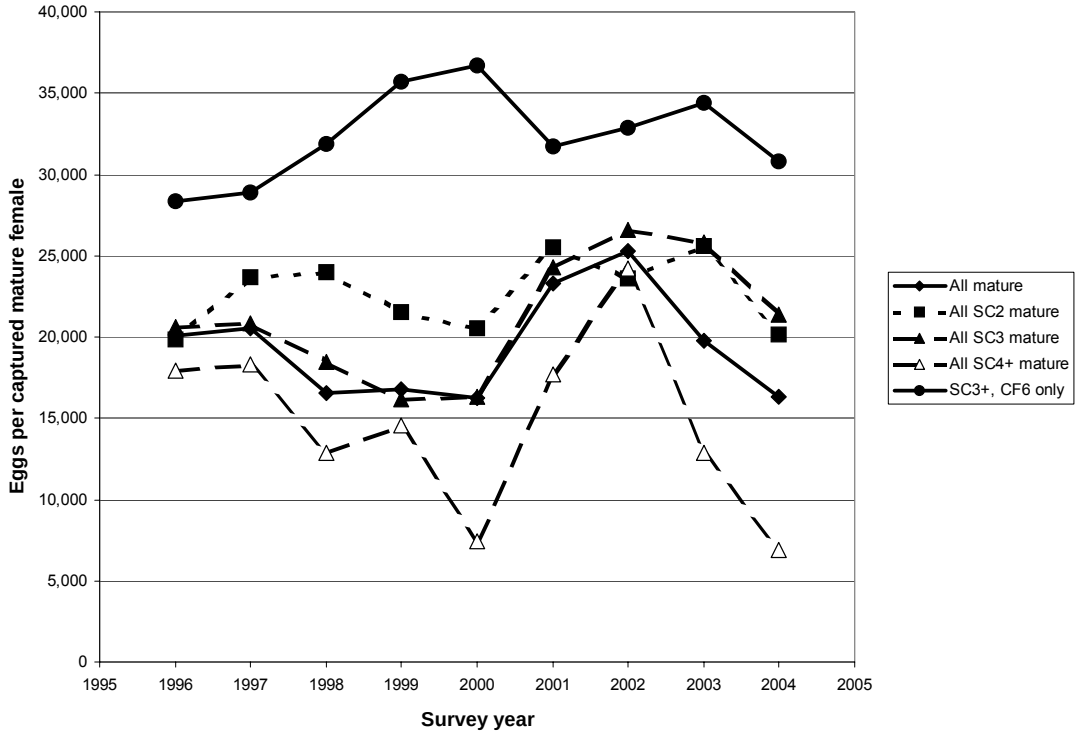

Figure 6. Estimated eggs per mature female snow crab captured annually during the 1996-2004 standard NMFS EBS trawl survey, by selected shell condition class and clutch fullness code combinations. (Source: Figure 13 of Rugolo et al. 2005).

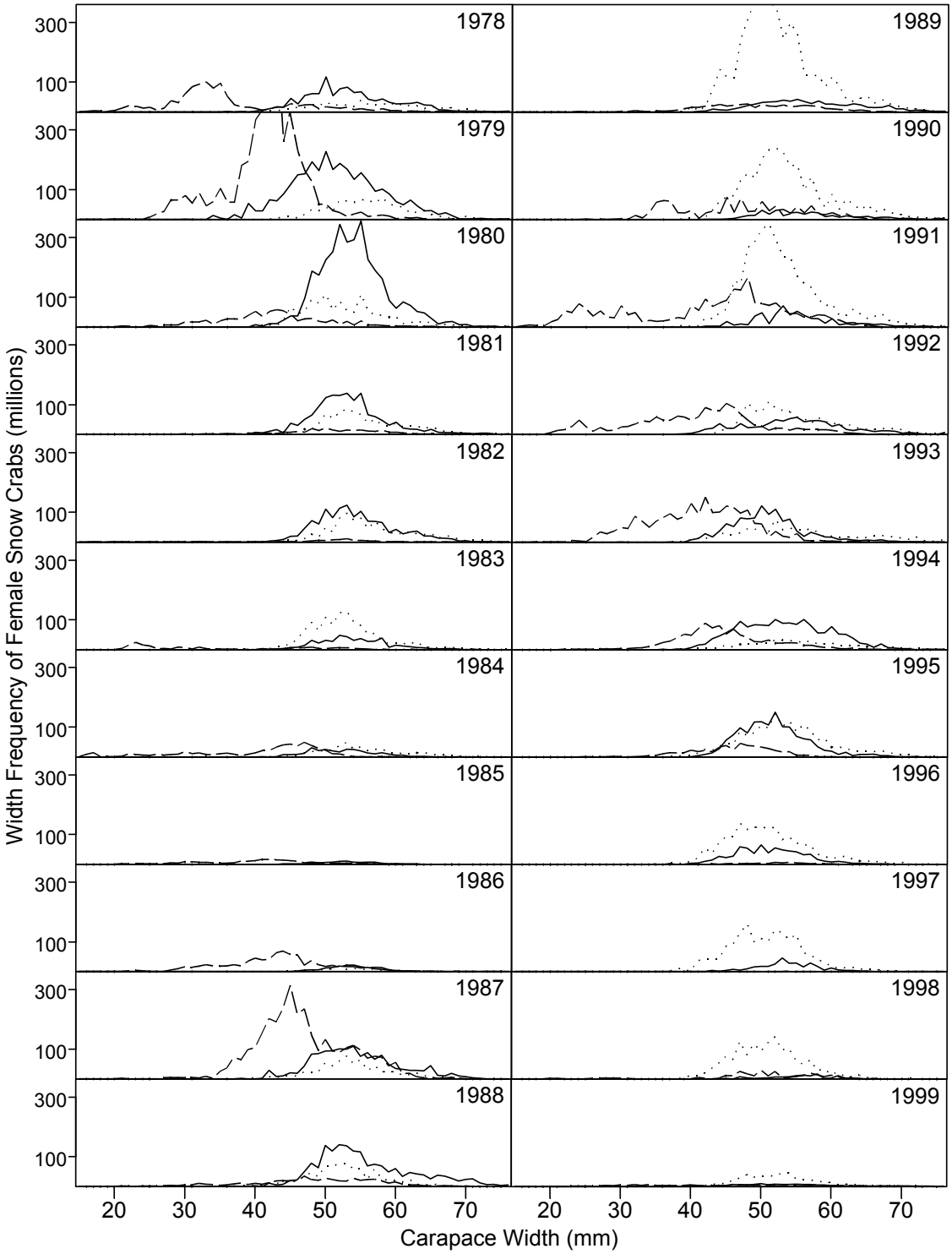

Figure 7. Width frequency of area-swept estimates of female snow crab abundance south of 61.2^{0}N in the eastern Bering Sea. Dashed lines---immature crabs, solid lines---newshell mature crabs, & dotted lines---oldshell mature crabs.

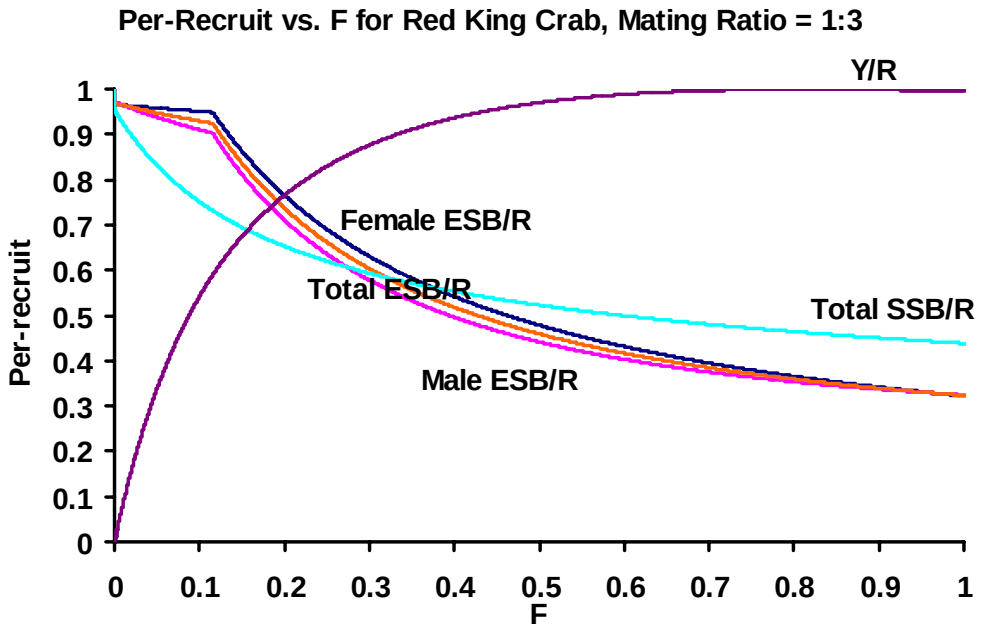

Figure 8a. Spawning biomass and yield per recruit for Bristol Bay red king crab for scenario 1.

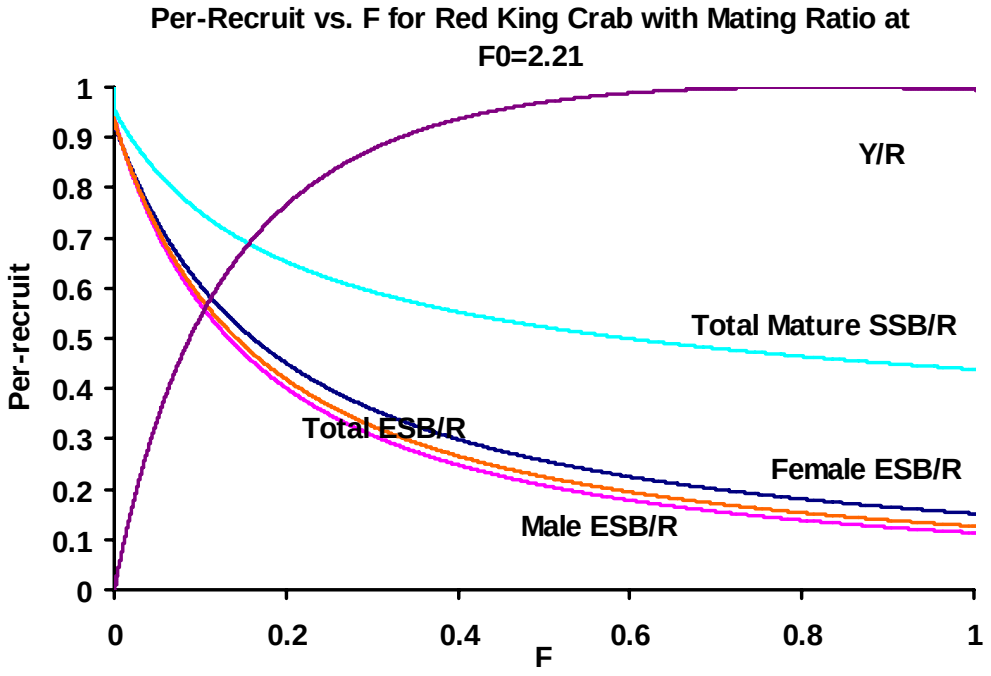

Figure 8b. Spawning biomass and yield per recruit for Bristol Bay red king crab for scenario 2.

Appendix A. Summary of "Powell's Kodiak red king crab grasping pair data" with regard to shell age of the males in the grasping pairs.
By Doug Pengilly, ADF&G

Back in the day, Guy Powell and his worker bees would estimate the shell ages to the nearest *month*(!). That might be kind of stretching the precision at which can estimate shell age, but most of the shell ages group around "1 month", "12 months," and "24 months" with a few months spread about the peek frequencies (Figure 1). For the purposes of the report on Powell's data that we did for the Sea Grant Symposium, we pooled the shell ages estimated in months into "new," "old", and "very old" as follows:

- New = 1-8 months
- Old = 9-16 months
- Very Old = 17 –36 months.

Given the distribution of shell age as estimated in months (Figure 1), I'm assuming that that classification means that:

- The "new shell" category corresponds with "molted shortly before or during the current mating season (which extends from at least January to May); i.e., whether the true shell age was 1, 2, or 3 months, it seems pretty clear that the recorder identified these crabs as having recently molted during the current season and not at the "tail end" of the preceding season.
- The "old shell" category corresponds with "last molted about one year before the current mating season.
- The "very old shell" category corresponds with "last molted two or more years before the current mating season.

Now, there's no way to give precise statements when pooling data from several years and several locations when the data was collected opportunistically and there was real unbalanced sampling by year, location, and month. However, these data sure indicate that males that molted during the current season can and did take part in mating behavior.

Grouping the data by month (Fig 2) indicates (acknowledging the warning of preceding paragraph) that the New Shells tend to get involved later in the mating season; i.e., they molted earlier in the mating season, but by April-May they were hardened-up enough to start grasping. And by April-May, those females they were grasping were mainly older multiparous females.

The data for January and February is limited in sample sizes and the years and locations (just from St. Paul Harbor and mainly from early 70's). There's very few New Shells males involved in the Jan-Feb grasping pairs. Most (84%) of the females in those early-season Jan-Feb grasping pairs were in their first mating. So, from this limited data, there is the suggestion that primiparous females are generally bred by Old, and Very Old

shells. It seems reasonable to guess that this is because the males have not yet molted to the "new shell state" or are in the processing of molting to, or have recently molted to, new shells and not available for grasping that early in the season. Who knows if those old and very old shell males that grasped females in January/February later molted and ended up with females in May as "new shells"?

Anyway, it looks like new shell males (i.e., those that have molted during the current season) can mate during the season that they have molted. Their representation among grasping pairs probably depend on whether or not they are around to take part in the mating and, maybe, whether or not there are a lot bigger, tougher old shell males to exclude them from mating.

I also included a histogram of the male sizes by shell age (Figure 3). I can't remember why and don't know if it shows anything except that these are mainly big males; the new shells tend to be smaller than the olders, but I'm not sure where to go with that, given the pooling of all the data.

Maybe need to get back to Guy Powell on molt timing of males…

-doug

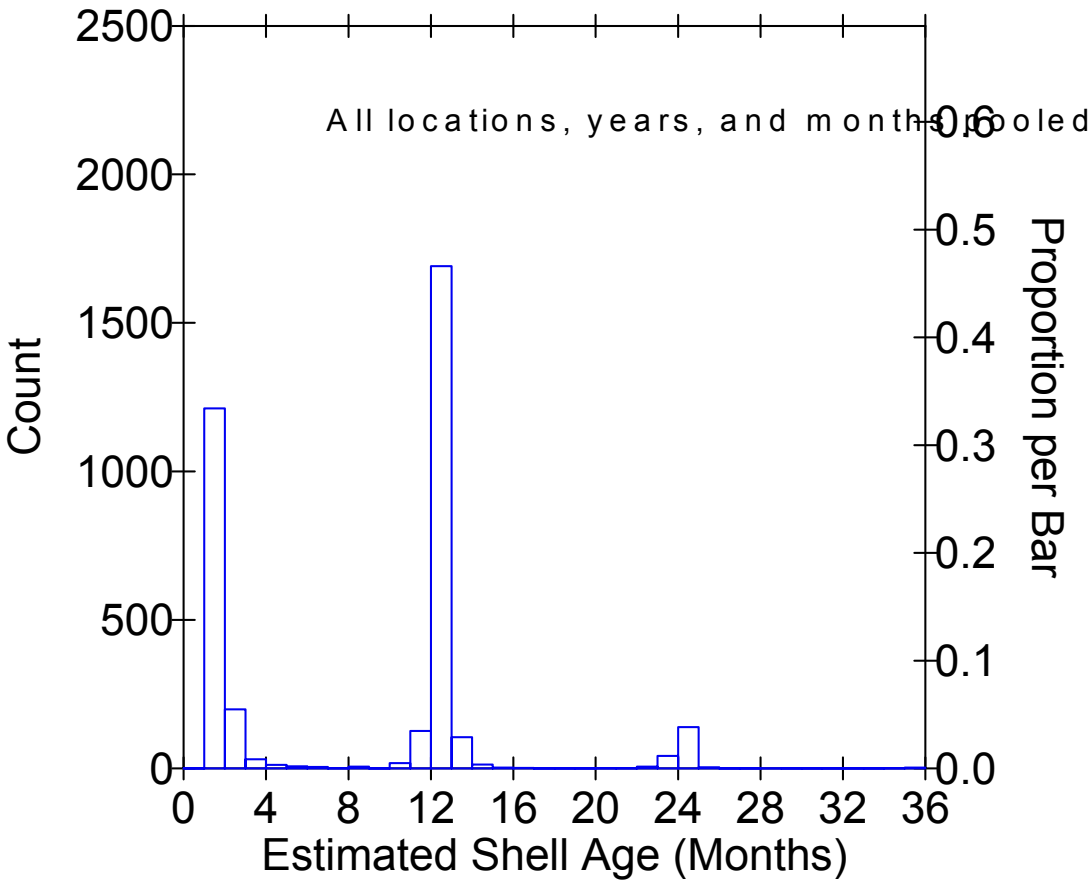

Fig 1. Histogram of shell ages estimated in months of red king crab males in grasping pairs; Powell's Kodiak data, all locations, years, and months pooled. (Graph doesn't include a handful of observations with shell ages of 36 months – I didn't want top extend the x-axis to 40. Also, sorry for the weird formatting of the in-setted text!)

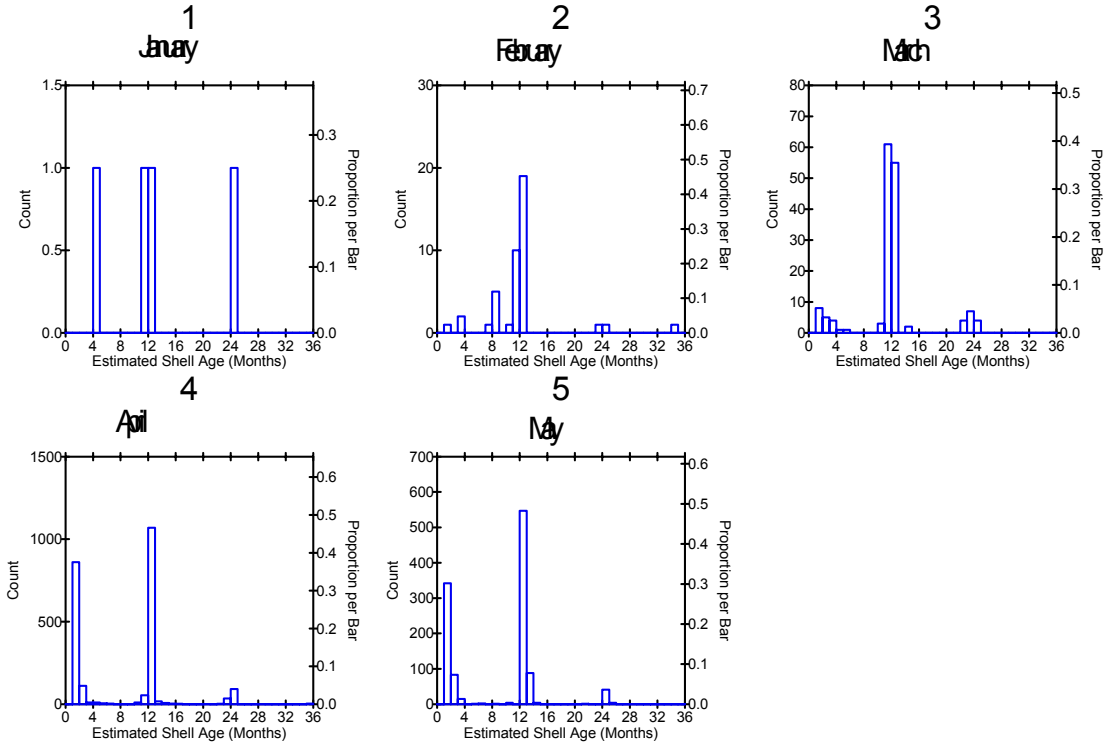

Fig 2. Histogram of shell ages estimated in months of red king crab males in grasping pairs by month of collection; Powell's Kodiak data, all locations and years pooled. (Graph doesn't include a handful of observations with shell ages of 36 months – I didn't want top extend the x-axis to 40. Also, sorry for the weird formatting of the text for names of months! They're supposed to read: "January," "February," "March," "April," and "May.")

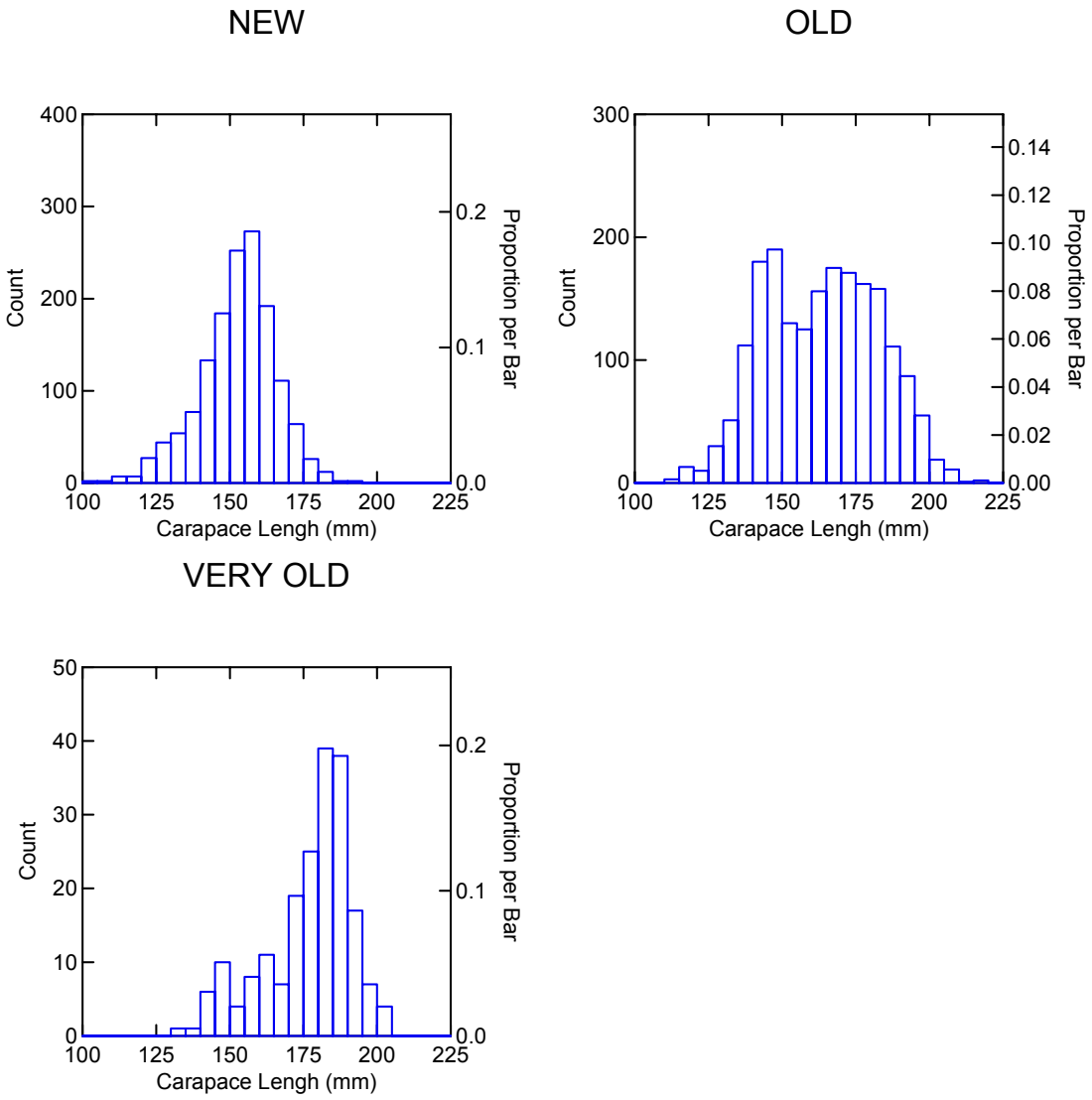

Fig 3. Histogram of carapace lengths by shell age (New = 1 to 8 estimated months, Old = 9 to 16 estimated months, Very Old = 17 to 36 estimated months) of red king crab males in grasping pairs; Powell's Kodiak data, all locations and years pooled. (A handful of CLs <100 were omitted so I could start the x-axis at 100).

Appendix B. Crab Mating and Molting – Response to Jie Zheng by Brad Stevens on April 8, 2005

JZ's Questions (in bold italic):
In your previous email, you indicated that the new egg clutches at survey are definitely fertilized for red king crabs and fertilized with a high (95-100%) probability for C. bairdi and snow crabs. So, basically, the new egg clutch information collected during summer survey can be used as an indicator of mating success.

BGS Response:
Female king crab will not extrude eggs if they have not been grasped and mated by a male within 13 days of the molt; about half of those mating between 9 and 13 days extrude eggs (McMullen, 1969); the author stated that all the extruded eggs were fertilized, though he did not assess this in any quantitative manner. However, Paul and Paul (Paul and Paul, 1990) showed that RKC with fertile clutches may contain some unfertilized eggs that adhere normally. In contrast, female Tanner crabs may extrude unfertilized egg clutches that attach to the pleopods and remain for some time after mating (Paul and Paul, 1992) furthermore, we cannot distinguish these by eye, so they would be recorded as if they were fertile.

The mating season is about from Jan. to March for primiparous red king crab females and from April to June for multiparous red king crab females in Bristol Bay.

That's probably correct. In a typical survey starting in early June (eg. 2002, 2004), 97-9% of female RKC have molted by the start of the survey. In years that are particularly cold, or when the survey started earlier (e.g. May 23 in 2000) large proportions of females are still carrying eyed eggs and must be re-surveyed later. Molting dates for Kodiak RKC are somewhat earlier. Powell (Powell et al., 1973) stated that he found "pubescent" (=primiparous) females in wild mating pairs between 14 Feb and 13 March 1971. "Adult females began molting and mating 23 April in the same general depth and locality …" (ibid, p. 81). Powell did not define how he distinguished "publescent/primiparous" females from "adult" crabs without observing them prior to molting. In our lab study, over two years, 12 adolescent females molted with a mean date of 4 Feb, and 24 multiparous crabs molted on a mean date of 30 March, plus or minus a week.

It appears that mature males molt mostly during March-May.

Despite much dogma about the timing of male molting and its frequency, there may be good reason to doubt much of it. Powell's 1967 ms is still the best source for this information (Powell, 1967). Looking only at tagged crabs that were released in Chiniak Bay in 1959, his data (table 7) show that molt frequency decreases with size. Of crabs that were at large for 2 years, 8% of those in the 87-100 mm range molted 3 times, and 92% molted twice; as juveniles multiple molts per year are expected. All crabs between 102-126 mm molted twice (annually). At sizes of 127-141, 45% of crabs molted only once, and all crabs >142 molted only once in two years. His discussion and table 14 on pp 47-48 contradict that interpretation somewhat, and I can't reconcile the differences between the two tables. However, he concludes (p. 49) that male crabs probably molt annually through age 7. At age 8 and 158 mm, they start molting biennially, and after two biennial molts, crabs enter a triennial molting phase at age 11-12. However Table 7 indicates that half begin biennial molting at 127-141 mm, and Table 14 indicates that it may start at 150 mm. Note, though that he recovered very few crabs larger than 150 mm.

Concerning seasonality of molting, Powell states that large adult males molt in April-May (p. 43), however the data in table 11 (p. 44) indicate that most crabs that molted in a given year were recovered in July-August, and about 1/3 were recovered in April-June, implying that the majority molted sometime between June and August. Therefore, if they participate in mating the following

year, they would be 7-10 months post-molt. Matsuura and Takeshita held 2 males through several successive molts (Matsuura and Takeshita, 1976); a small (85 mm CL) male molted annually between Nov. and Feb until reaching a size of 136 mm; a larger (118 mm Cl) male molted in February, then again 22 months later. However, this is a small sample of crabs held in a laboratory which may affect molt interval. According to Pete Cummiskey, a large proportion of adolescent males undergo their maturity molt in late summer or fall in Women's bay, out of sync with the females; in his database, 10 of 20 sonic-tagged male crabs over 90 mm molted in Aug-Sept, not to mention many untagged molts that were observed. Presumably, they are hard enough to mate the following spring. His data are more-or-less consistent with Powell's, though they demonstrate a slightly later molting time. My interpretation of these sources is that some males molt to maturity at the same time and age that the females do, but mature males subsequently molt in the summer, out of sync with the females.

If there is no space separation, mature males can mate with primiparous females first and then molt. There are two lab studies (Powell et al. 1973; Paul and Paul 1990) to indicate that males can mate after 10 days or 2 weeks of molting. If this is the case, almost all mature males (newshell and oldshell at survey time) have a time window to mate with both primiparous and multiparous females before the survey. From your email to Siddeek, you think that males can mate before they molt in the spring, but cannot mate at least within 6 months after molt.

Your citations are correct, but I would be cautious about applying them to natural populations. Powell et al. (Powell et al., 1973) placed 20 recently molted males in pens with females, and 10 of those males mated after a minimum of 6 days post-molt. In addition, 37 of 42 small males (over half of which were <100 mm CL) mated with females much larger than themselves in 4x4 ft enclosures. However, some of Powell's results with paired crabs in closed pens contradict his observations of crabs in the wild, and such pairings are so rare in nature as to be practically non-existent. For example only 6 males <110 mm were found among 3,402 grasping pairs captured in the wild. Since the SM_{50} reported for females in his study was about 106 mm, and males averaged 42 mm larger than their partners, there is an extremely low probability that females are fertilized by such small males in the wild. In addition, his crab tagging data show that most large males molted in the summer, so would not participate in mating for another 7-10 months.

Powell et al. (Powell et al., 1974) reported mating between females and "new-shell" males, but he did not define shell conditions. In their 1973 paper, they identified the shell age of male crabs to the nearest month (eg, 8, 9 10, or 11 months). I seriously doubt the accuracy of such visual shell aging techniques and suspect they were based on the presumption of spring/summer molting. Studies of radiometric aging have shown that such techniques can be very uncertain, especially for old shells (codes 4 and 5 in the NMFS scale); estimated ages of shell 4 crabs ranged from 4 to 7 years (Le Foll et al., 1989; Nevissi et al., 1996). But even if they were correct, 8-11 months may be enough of a time lag after molting, whereas Powell did not find any wild pairs with male crabs <8 months post-molt, by his estimate.

Early experiments with snow crab also showed that small males could mate with mature females in aquaria, but many studies with both snow and Tanner crabs (e.g.\ (Stevens et al., 1993) have since shown that large-clawed old-shell males constitute the vast majority of functionally mature maters in wild populations (see below). It is unlikely that male snow or Tanner crabs mate in the year that they undergo their maturity molt.

I doubt that males participate in mating soon after molting, in a natural situation with other competitors. For one reason, it takes a long time to recover hardness after molting; we tested shell hardness last year for 35 RKC over 90-120 days, and found that only half regained their pre-molt hardness levels during that time interval. Soft shelled crabs are at a great mechanical disadvantage. Feeding rates are significantly lower for about 2 weeks before and after molting

(Zhou et al., 1998). For another reason, it is likely that mature male crabs molt several months after the females in any given year. For your modeling purposes, the question really is: Have male RKC that are coded as shell 2 in the survey participated in mating? The answer is probably yes.

Based on an assumption that the 50% maturity for Bristol Bay male red king crabs is 120 mm CL,

That may be about right for functional maturity. The size at 50% morphometric maturity is 102.8 mm according to Somerton (1980), physiological maturity is even smaller (Paul, 1992), but the minimum size of males seen in grasping pairs was >110 mm (Powell et al., 1973).

The sex ratios from 1972 to 2004 range from 2 to 35 mature females to 1 oldshell mature male and 1 to 4 mature females to 1 mature males (combined newshell and oldshell). Even without data before 1983 (assuming underestimating oldshell males), the highest sex ratio is still 8.2 mature females per mature oldshell male. The new clutch fullness from 1975 to 2004 ranged from 62% to 98% with a mean close to about 90%. Basically, lack of mature males was not much of a problem for Bristol Bay red king crab based on the new egg clutch data. So, if only oldshell males can mate, then a male may need to mate with up to 8 females to produce these egg clutch data. If assuming one oldshell male can mate with only 2 females each year, then up to 70% or 75% of mature females could not be mated due to lack of males in some years. If both newshell and oldshell males can mate, then a mating ratio of one male to 2 females can produce the egg clutch we saw during the summer survey. Would you please comment on these three assumptions for a mating season:

(1) only oldshell males mate and one male can mate up to 6 females;

You are giving too much significance to shell conditions. Shell 2 does not necessarily imply that the crab recently molted. If males molted in the late summer or fall (as in Women's Bay), they could be hard-shelled enough to mate by the following spring. During the ensuing summer survey, we would code them as shell 2 (newshell) even though they might be anywhere from 3 to 18 months post-molt. They would not earn a shell 3 (old-shell) until at least 1.5 years or longer after molting.

(2) only oldshell males can mate and one male can mate up to only 2 females;

This is apparently not correct. It is likely that a large portion of male crabs coded as shell 2 participate in mating. Also see below.

(3) both newshell and oldshell males can mate and one male can mate up to only 2 females.

Most of the mating experiments have compared small to large crabs. Powell et al. (1974) stated that both "new-shell" and "old-shell" males could mate up to 7 females successfully, and some males mated with as many as 13, though fertility rates fell off after the 7th mate. However, his "small new-shell" male was 135 mm (barely sub-legal) and he did not define "new-shell", which could simply be any male that molted within the past year (in March, when the study was done, such males probably molted 6-12 months prior). According to Paul and Paul (1990), males of

110-119 fertilized one mate successfully, but only 72% of their second mates, with 74% fertilization (essentially 1.5 successful matings), whereas males >120 fertilized 4 mates successfully. Hard old-shell males >140 mm fertilized 3 mates successfully and 6 of 10 fertilized their fourth mates. Therefore I think it is safe to say that males >120 mm can fertilize 4 females successfully, whether they are shell 2 or shell 3.

For EBS snow crabs, clutch fullness from 1975 to 2004 is often from 60% to 90% for newshell and oldshell females and 40% to 80% for very very oldshell females. Sex ratios range from 5 to 71 mature females (a median of 27) to one mature oldshell male and 1 to 14 mature females (a median of 5) to one mature male (newshell and oldshell combined). Let's ignore sperm storage feature because most computer simulations ignore it. Would you please comment on the assumptions for a mating season:

(1) only oldshell males can mate…
Unlike red king crab, in the genus *Chionoecetes* all indications are that old-shell, large-clawed males predominate in mating pairs. Mean size of males mating with new-shelled (primiparous) female Tanner crabs was 107 mm, and of those mating with old shell (multiparous) females was 132 mm; 57% of the former, and 90% of the latter males were old-shell (Stevens et al., 1993). Only old-shell males >114 mm successfully fertilized multiparous females in captivity, and those with 1 claw were successful in 7 of 9 tests (Paul and Paul, 1996). When paired OS and NS male Tanners of equal size (all with large claws) were given simultaneous access to females, the female mated with the OS male 70% of the time; new-shell males up to 99 days post-molt did not copulate with either multiparous or primiparous females (Paul et al., 1995). We generally assume that these results extend to snow crab.

… and one male can mate up to 9 females;
Unlikely. In the lab a single male Tanner crab fertilized 10 females, but the sample size was only 1; other crabs fertilized 3 to 4 females (Paul, 1984).

(2) only oldshell male can mate and one male can mate up to 4 females;
This looks like a reasonable number (see above).

(3) only oldshell male can mate and one male can mate up to 2 females;
See above.

(4) oldshell mature males and 30% newshell mature males can mate and one male can mate up to 3 females.
We have already established that old-shell, large-clawed males breed with multiparous females, although some new-shell males can mate with primiparous females. New-shell, in this context, is a shell 2, which probably indicates a crab that molted 6-12 months previously; it does not include crabs that molted less than 3 months previously. Therefore, I would conclude that
1) only large-clawed (morphometrically mature) males participate in mating;
2) old-shell (shell 3 or greater) males mate with 90% of the multiparous females, and can mate with 3-4 females per season;
3) new-shell (shell 2) males may mate with some (up to half) of the primiparous females, probably at a reduced rate (1-2 per season?). This is probably a result of separation of cohorts by age, and may be highly dependent on the ratio of new/old shell crabs in the immediate vicinity (10 mile radius).
4) None of this can be used to predict the proportion of new- or old-shell males that participate in mating. Based on our observations in Chiniak Bay, it is likely that a large portion of the male stock does not get close enough to female aggregations to participate in mating at all.

Another thing puzzling me is that there are almost no oldshell mature males north of 61.2 degree at the survey time, but mature females have very good egg clutch there. Is it more likely that oldshell males mate and then move south before the summer survey, or some mature newshell males can mate there?

In 2004, >85% of ovigerous females and 92% of males North of 61.2 N Lat, were shell 2. Chela measurements were not taken on ANY males at that latitude. However, chela measurements were taken on 308 males (representing 695 individuals) north of 59.9 Lat. I used a cutline defined by Rugolo, Pengilly et al. (courtesy of R. MacIntosh) to determine their maturity (see attachment). Of those crabs, 58% were shell 1-2; of those, most crabs <100 mm CW were small-clawed (below the cutline), but the majority >100 mm CW were large-clawed. 42% were old-shell (shell 3-5) and 97% of those were large-clawed. Even though those data were collected south of 61 Lat, they indicate that

1) There are quite a few old-shell males between 60 and 61 N lat, and
2) Many of the newshell males are morphometrically mature.
3) Based on what we know, and the uncertainty of shell definitions, it's possible that some of the females there were mated by new-shell males.

This is a long message and thanks very much for your time and effort. Your comments will help us to get a better definition of overfishing/overfished because the results from computer simulations are largely dependent on these assumptions.

Mucho gusto, doitashimashite.

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