

Estimating king crab (*Paralithodes camtschaticus*) abundance from commercial catch and research survey data

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Abstract: Reliable estimates of male abundance are required to set harvest guidelines for red king crab (*Paralithodes camtschaticus*). Data available for population estimation include commercial catch and relative abundance estimates from research surveys. Although absolute age of king crabs cannot be determined, shell age and size can be used to classify legal-sized crabs into recruits and post-recruits. We modified a method of catch-survey analysis, originally developed by Collie and Sissenwine, for estimating legal male king crab abundance. The method scales the relative abundance index to the commercial catch data and smoothes the abundance estimates by accounting for errors in measuring relative abundance. We conducted Monte Carlo simulation trials with known data sets to test the precision and accuracy of this estimation method and its sensitivity to violations of the underlying assumptions. Bias in the abundance estimates was less than 5% for realistic levels of measurement and process errors. The simulation framework was used to calculate bootstrap estimates of population abundances. We applied the method to estimate the abundance of Kodiak and Bristol Bay red king crabs. In the early 1980's, dramatic declines in the abundances of both stocks coincided with decreasing recruitment and high harvest rates. The decline in Bristol Bay was compounded by a sharp, temporary increase in natural mortality.

Résumé : Une estimation fiable de l'abondance des mâles est nécessaire pour établir les règles régissant la récolte du crabe royal (*Paralithodes camtschatica*). Les données disponibles pour estimer la population comprennent les valeurs estimées des prises commerciales et de l'abondance relative provenant des relevés de recherche. Bien qu'on ne puisse déterminer l'âge absolu du crabe royal, l'âge et la taille de la carapace peuvent être utilisés pour classer les crabes de taille légale en recrues et post-recrues. Nous avons modifié une méthode d'analyse prises-relevé, élaborée initialement par Collie et Sissenwine, pour estimer l'abondance du crabe royal mâle de taille légale. La méthode établit une correspondance entre l'indice d'abondance relative et les données sur les prises commerciales et ajuste les valeurs estimées de l'abondance en tenant compte des erreurs liées à la mesure de l'abondance relative. Nous avons réalisé des essais de simulation de Monte Carlo avec des ensembles de données connues pour vérifier la fidélité et la justesse de la méthode d'estimation et sa sensibilité aux violations des hypothèses sous-jacentes. L'erreur touchant les valeurs estimées de l'abondance était inférieure à 5 % pour des degrés réalistes d'erreur de mesure et de méthode. Le cadre de simulation a été utilisé pour calculer des valeurs estimées par auto-amorçage des abondances de population. Nous avons appliqué la méthode pour estimer l'abondance du crabe royal de l'île Kodiak et de la baie de Bristol. Au début des années 80, un déclin marqué de l'abondance des deux stocks a coïncidé avec une diminution du recrutement et une augmentation des taux de récolte. Le déclin dans la baie de Bristol a été aggravé par une augmentation brusque et temporaire de la mortalité naturelle. [Traduit par la Rédaction]

Introduction

Most red king crab (*Paralithodes camtschaticus*) fisheries in Alaska are currently managed with an exploitation rate strategy in which annual catches of legal-sized males are prescribed by applying a harvest rate toward estimates of spawning male biomass (Kruse 1993). Abundances of red king crab populations have been estimated by annual stock assessment surveys.

Since 1968, the National Marine Fisheries Service (NMFS) has used area-swept methods to calculate trawl-survey indices of absolute abundance of Bering Sea stocks (Otto 1986). During the 1970's through late 1980's, relative abundances of Gulf of Alaska stocks were estimated with pot surveys conducted by the Alaska Department of Fish and Game (ADF&G). For a few stocks, absolute abundances of legal males were estimated by Petersen estimators applied to tag-recapture data (Blau 1985). With the exception of stocks in Southeast Alaska, where topography prevents trawling in most king crab habitats, ADF&G switched to trawl area-swept methods in the late 1980's. Occasionally, alternative methods based on inseason changes in fishery catch per unit effort (Leslie and Davis 1939) have been attempted (Otto 1986), but these have not been used routinely for assessments or for fishery management.

More recently, alternative methods incorporating an underlying population model have been applied. These methods are catch-survey analysis (CSA, Kruse and Collie 1991) and length-based analysis (LBA, Zheng et al. 1995). The advantages of the LBA over CSA are that it can be applied to females as well as males and it more fully utilizes data on size and shell

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condition of crabs in the survey and commercial catches. The population dynamics model underlying CSA is more parsimonious, which makes it less data intensive, and therefore it can be applied to a wider range of sampling situations. We believe it prudent to apply multiple approaches in any one case to develop confidence in the various alternative estimation methods.

In this paper, two red king crab stocks are analyzed: one residing around Kodiak Island in the Gulf of Alaska and one in Bristol Bay in the eastern Bering Sea. These two stocks once supported the two largest king crab fisheries in the world. Small catches of red king crabs were first delivered to Kodiak in 1936, but landings were not recorded until 1950 when 27 t were landed (Spalinger and Jackson 1994). Annual landings peaked at 43 000 t in 1965, stabilized at 5 000–11 000 t in the late 1960's until the early 1980's when landings declined sharply. The fishery has been closed since 1983 due to extremely low stock abundance. Red king crabs in the eastern Bering Sea were exploited by Japanese fisheries from 1930 to 1940 and 1953 to 1974. Russian fisheries operated during 1959–1971 (Morrison and Gish 1994). Early U.S. red king crab explorations began in the early 1940's (Anonymous 1942). A small domestic fishery began in 1947, but domestic landings remained low until the 1970's when the foreign fishery was phased out (Morrison and Gish 1994). Total annual landings from Bristol Bay were <6100 t in the 1950's, 11 100–29 000 t in the 1960's, and 8 700–49 000 t in the 1970's. Landings peaked at 59 000 t in 1980 and declined sharply in the early 1980's. The fishery was closed in 1983 due to low abundance. During 1984–1993 annual landings were 1900–9200 t. The Bristol Bay fishery was again closed in 1994 due to low abundance; a small harvest (600 t) was taken from the Pribilof Islands area of the eastern Bering Sea.

The population estimation method described in this paper is called catch-survey analysis (CSA) because it calibrates relative abundance to absolute abundance and smoothes variability in the relative abundance data. The method is derived from the classic depletion estimators of Leslie and Davis (1939), which have long been used to estimate the abundance of invertebrate populations such as lobster (DeLury 1947). For a closed population, the catchability is estimated from the decline in catch rate and then used to estimate initial abundance. In applying depletion estimators to whale populations, Allen (1966) and others modified the methods for open populations with recruitment and natural mortality. Collie and Sissenwine (1983) developed a two-stage model for stocks that can be classified into recruits and post-recruits and applied it to east coast groundfish stocks for which the full age structure was unknown. Kruse and Collie (1991) adapted CSA to king crabs (for which age cannot be determined); the method has since been used to estimate the abundance of red king crabs in Southeast Alaska (Woodby 1994). With further refinements, CSA has been used to assess the abundance of Atlantic sea scallops, *Placopecten magellanicus* (Conser 1991), and American lobster, *Homarus americanus* (Conser and Idoine 1992).

Collie and Sissenwine (1983) recommended testing the reliability of CSA on simulated data sets for which true abundance is known. Although the method has become more widely used, its performance has not yet been tested with Monte Carlo simulations. In this paper we test the sensitivity of CSA to violations of the input assumptions and to the

magnitude and form of residual errors. Finally, the simulation framework is used to calculate bootstrap estimates and confidence intervals.

Methods

Abundance and landings data

Time series of pot surveys (Kodiak) and trawl surveys (eastern Bering Sea) afford contrast in application of our approach. The Kodiak pot survey was described in detail by Peterson et al. (1986), and historical commercial landings were reported by Spalinger and Jackson (1994). We gathered pot survey and landings data for 1973 to 1986. Since 1986, surveys have been conducted by trawl rather than pot gear. We confined our Kodiak analysis to the period spanning the pot-survey data series because pots and trawls have different catchabilities and because the lack of a fishery since 1983 prevented use of commercial catch data to estimate the trawl catchability coefficient. We regarded Kodiak red king crabs as one stock because (i) they are managed as a single unit (Spalinger and Jackson 1994), (ii) crab habitats around Kodiak Island are distinct from adjacent areas on the mainland, and (iii) isozyme analyses indicate genetic differentiation among broad provinces (e.g., Gulf of Alaska, Aleutian Islands, Bering Sea) rather than within smaller geographic areas (Seeb et al. 1990).

The eastern Bering Sea trawl survey was described in detail by Otto (1986), and historical landings were reported by Morrison and Gish (1994). We obtained trawl survey and landings data for 1975 to 1994. Red king crabs from the eastern Bering Sea occupy two semi-discrete areas: Bristol Bay and the Pribilof Islands. The Pribilof Islands have accounted for an extremely small fraction of overall historical red king crab abundance in the eastern Bering Sea; no directed fishery occurred except in 1993 and 1994 when small catches (1200 t and 600 t, respectively) were taken. This being the case, combined abundances of red king crabs from the two areas are routinely reported by NMFS in annual stock assessment documents (e.g., Stevens et al. 1994). To compare our results to published abundance estimates, for purposes of this analysis we treated red king crabs from the eastern Bering Sea as a single stock and hereafter refer to them as Bristol Bay.

Crabs caught during surveys were classified based on commonly used measurements of size and shell condition. "Carapace width" (CW) is the greatest straight-line distance across the width of the carapace including spines, whereas "carapace length" (CL) is the distance from the posterior margin of the right eye orbit to the posterior carapace margin. Legal crabs are males ≥ 178 mm CW (≈ 145 mm CL) for Kodiak and ≥ 165 mm CW (≈ 135 mm CL) for Bristol Bay (ADF&G 1994). Shell condition (e.g., discoloration, wear, presence of barnacles) allows biologists to classify crabs as "newshell," those that molted within the past year, and "oldshell," those that have molted more than a year previously. Shell size and condition are used to categorize legal crabs as "recruits," those that have been legal for only one year, and "post-recruits," those that have been legal for more than one year. Recruits are newshell crabs between legal size and one mean growth increment larger than legal size. Post-recruits are all remaining legal crabs. For Kodiak, recruits are newshell crabs ≥ 145 mm CL and < 165 mm CL, whereas for Bristol Bay, recruits are newshell

water in February–May, we computed annual anomalies of 50-m temperatures in the following way. First we computed long-term monthly mean temperatures for the period 1971–1994, and then computed monthly anomalies by subtracting the long-term monthly means from the monthly mean temperatures for each year. The annual temperature anomaly was computed as the mean of the February–May monthly anomalies. There were three years in which no February–May temperature observations were made: 1973, 1980, and 1981. For these years, we computed temperature anomalies by linear interpolation from adjacent years.

Unfortunately, no routine subsurface temperatures are available for Bristol Bay from February to May. However, bottom-temperature data are collected during the annual NMFS trawl survey, typically conducted during June and July. Stevens et al. (1994) calculated a bottom-temperature index by computing the mean bottom temperature from 36 shallow-water (35–75 m) stations located just north of the Alaska Peninsula. From these data we computed annual bottom-temperature anomalies by subtracting the long-term (1971–1994) mean from Stevens' annual bottom-temperature index. The temperature anomalies were scaled to a mean M of 0.36 and a standard deviation of 0.15 to give maximum variability while ensuring that none of the annual M_t values would be negative.

CSA was performed with the three different mortality schedules, and in each case, the same number of parameters was estimated. On output, the relative abundance estimates (r_t and p_t) were divided by q to obtain the absolute abundance of legal crabs, $\hat{R}_t + \hat{P}_t$ (from eq. 2). Annual harvest rates (h_t) were calculated as the catch divided by the number of legal crabs at the time of the fishery:

$$[6] \quad h_t = \frac{C_t}{(\hat{R}_t + \hat{P}_t)e^{-M_t T}}$$

Sensitivity of CSA to input data and assumptions

We tested how well the model performs with a known data set, without error, based on the 20 years of data estimated for Bristol Bay. First, we tested how errors in the input parameters affect the estimation of the output parameters, especially q . We focus on q because division of relative abundance by the wrong q will result in biased absolute abundance estimates. We measured the deviation in estimated q from its known value of 1.0, with errors in the input values of T , M , and ϕ .

Next we tested the sensitivity of CSA to errors in classifying recruits and post-recruits. The magnitude of these errors can be estimated from crabs tagged by ADF&G biologists during summer surveys and recovered by ADF&G technicians during the fall/winter fishery. Molting did not occur during this period, so the tagged crabs should have the same size and shell age as they did when tagged. The size measurements were accurate to ± 1 mm, but errors in shell aging apparently did occur. If we assume that the original survey classification was correct, 3% of the recruits were later misclassified as post-recruits and 3% of post-recruits were misclassified as recruits (Blau 1988). These misclassification rates were used to calculate observed relative abundance of recruits (r_{obs}) and post-recruits (p_{obs}) with aging errors in each year.

$$[7] \quad r_{\text{obs}} = 0.97r + 0.03p$$

$$p_{\text{obs}} = 0.03r + 0.97p$$

We then tested the ability of CSA to estimate the original correct values. We consider these to be worst-case estimates of the misclassification rates in the survey because the resampling was done by technicians with less experience than the ADF&G biologists who conducted the survey. Also, the resampling occurred during the fishery which is later in the molting cycle when newshell crabs become progressively darker, scratched, and more difficult to distinguish from oldshell crabs.

The next step was to test how the magnitude and structure of the residual errors affect parameter estimation. The Monte Carlo simulations start with the same known data set with no error. The known data were modified with lognormally distributed random errors of the form $\exp(\epsilon - \sigma^2/2)$, where ϵ is a random normal deviate with mean 0 and standard deviation σ . The factor $\sigma^2/2$ ensures that the lognormal errors have mean 1. We tested three types of error structure (a) measurement errors as assumed in fitting the model with eq. 4, with $\sigma = 0.1, 0.3, 0.5, 0.7$, and 0.9 ; (b) correlated measurement errors as might occur because the observed \tilde{r} and \tilde{p} each year come from the same survey (the input correlation between η_t and δ_t was 0.5); and (c) process errors, which could result from year-to-year variations in M or errors in estimating C (in this case the population dynamics eq. 3 was multiplied by lognormal errors with $\sigma = 0.1, 0.3$, and 0.5). In addition to trials with single sources of error, trials were run with mixed levels of measurement and process errors and also with an assumed 10% error in classifying recruits and post-recruits (as in eq. 7, but with larger errors). Regardless of the structure of the input error, the same measurement-error model was used for parameter estimation (eq. 5). The randomization process was repeated 200 times and the results summarized according to the bias and dispersion of the parameter estimates.

Finally, the Monte Carlo simulation structure was modified to provide bootstrap estimates of the bias and dispersion of abundance estimates in each year. The first pass through the CSA used the observed data set. The result of this fit was the input data for the parametric bootstrap. These data were modified with measurement errors that had the same standard deviation as the observed residuals. The results of 1000 random trials were summarized by the mean and the empirical 95% confidence interval.

Results

Observed and estimated recruits and post-recruits for Bristol Bay red king crabs are in general agreement (Fig. 1). Changes in post-recruit abundance are offset by one year from the recruits as predicted by the population dynamics model (eq. 3). There is a temporal pattern in the residuals of the constant- M fit. In early and later years the model overpredicts recruits and underpredicts post-recruits; in middle years the opposite is true. This pattern suggests that natural mortality was above average from 1981 to 1985 and below average in the early and later years. The variable- M fit accounts for this shift and fits the observed data much better, with $q = 0.95$ and a reduction in the sum of squared residuals (SSQ) to 1.293 (Table 1).

The population model smoothes year-to-year variability in

Fig. 1. Abundances of Bristol Bay red king crabs measured with a trawl survey and estimated with catch-survey analysis. The constant M was 0.36 and the variable M s are from Zheng et al. (1995).

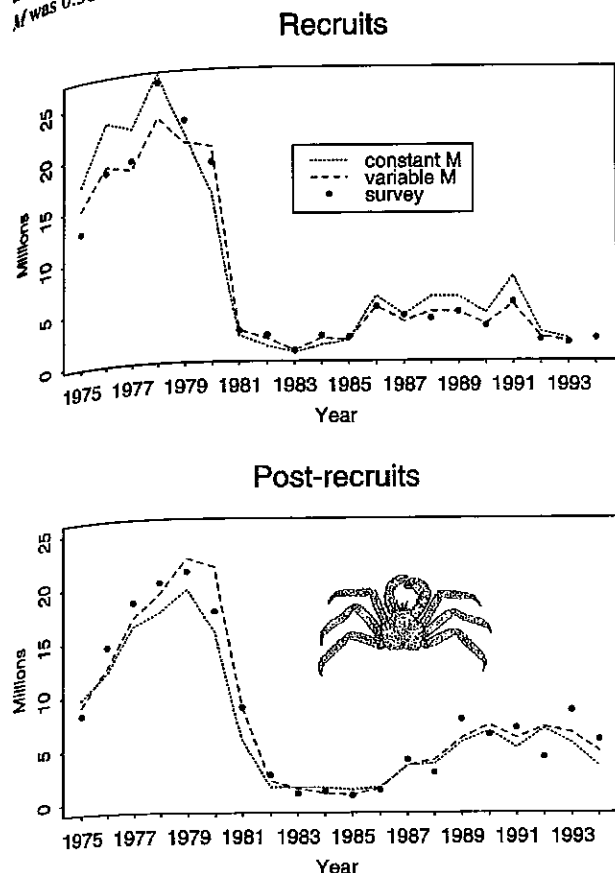


Fig. 2. Legal male abundance, harvest rate, and natural mortality of Bristol Bay red king crabs.

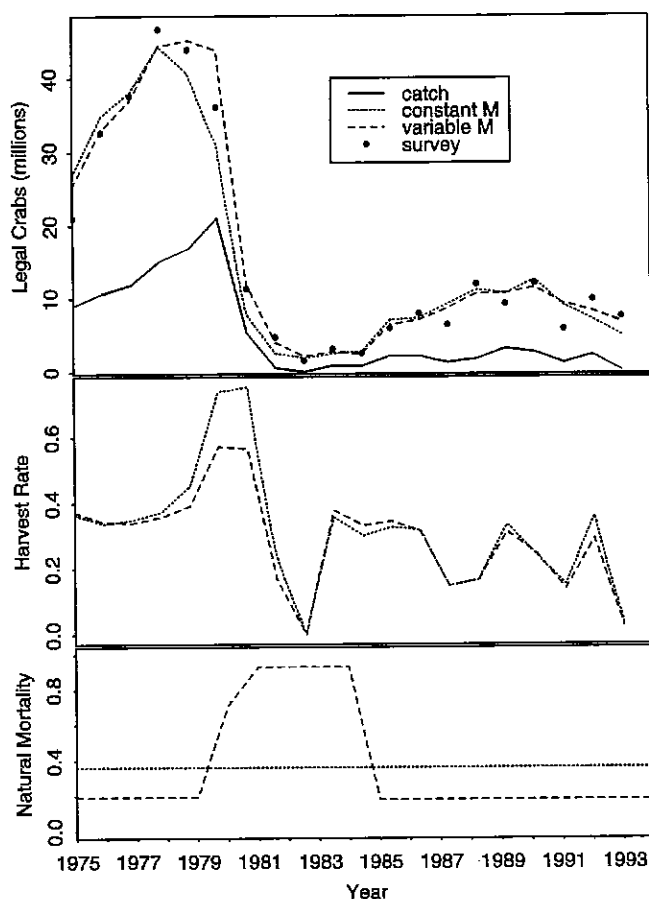


Table 1. Residual analysis of catch-survey analysis fits to Bristol Bay and Kodiak data with constant natural mortality.

Statistic	Bristol Bay	Kodiak
Number of years	20	13
Catchability coefficient (q)	1.01	0.97
Standard error of q		
linear approximation	0.58	0.31
bootstrap	0.15	0.10
Sum of squared residuals (SSQ)	4.313	1.009
Standard deviation of residuals	0.49	0.30
Kendall's rank correlation (τ) between recruit and post-recruit residuals	0.041	0.091
probability $\tau = 0$	0.807	0.681
First-order autocorrelation of residuals		
recruits	0.70	0.22
post-recruits	0.56	-0.29

the observed abundance estimates. A small increase or decrease in abundance can make the difference of the fishery being open or closed because thresholds are used to protect depressed stocks. If the increase or decrease were actually a measurement error, a management decision could also be made in error. Recruit abundance is not predicted in the final year because of the recursive nature of the population equation

(eq. 3). To estimate legal abundance we must rely on observed recruits in the final year.

Estimates of legal crab abundance are superimposed on the survey data along with the commercial catch (Fig. 2). Large catches were extracted from the large stock that existed from 1975 to 1980, prior to the crash in 1981. The fishery was closed in 1983 and continued at low levels until 1994, when only a small catch was taken around the Pribilof Islands. The collapse was caused by a combination of high harvest rates and an apparent increase in natural mortality. With the variable- M fit, harvest rates were still high leading up to the crash, but more of the deaths were attributed to natural causes. Recruits which were there one year disappeared by the next. The instantaneous natural mortality rate apparently increased to almost one. The trial with M scaled to sea-temperature anomalies did not improve the fit ($q = 0.87$, $SSQ = 4.478$) because the increase in temperature preceded the apparent increase in M .

Kodiak can be considered a test data set because there was no calibrated trawl survey for this stock to give a prior estimate of q . We performed two runs, one with constant natural mortality and one in which M was scaled to anomalies in subsurface temperature in the Gulf of Alaska ($q = 1.00$, $SSQ = 0.617$). The fit with variable M was improved in earlier years (Fig. 3), because the decline in abundance coincided with the increase in ocean temperature in the Gulf of Alaska. Observed high recruitment in 1979 could be considered a

Fig. 3. Relative abundances of Kodiak red king crabs measured with a pot survey and estimated with catch-survey analysis. The constant M was 0.36 and the variable M s were scaled to ocean temperature anomalies.

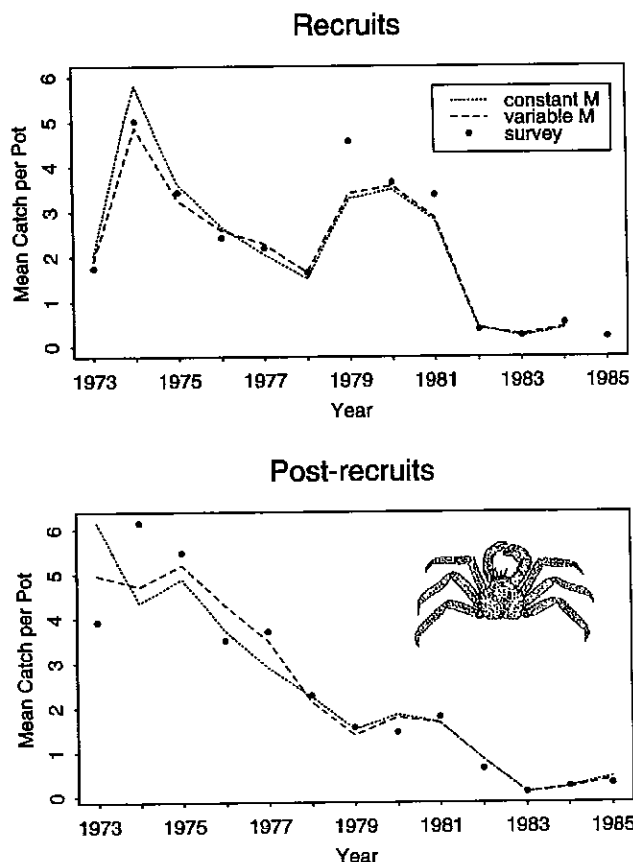
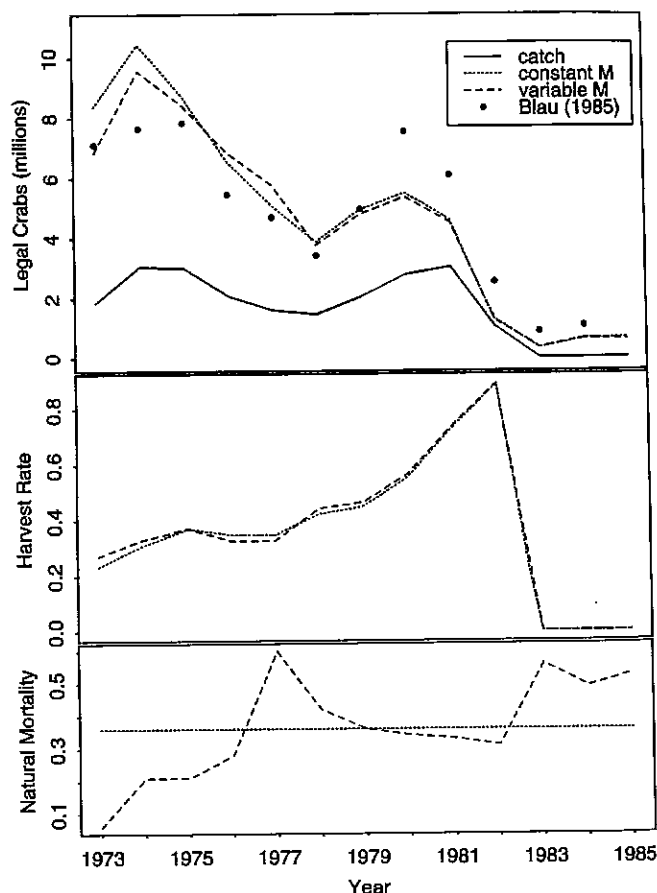


Fig. 4. Legal male abundance, harvest rate, and natural mortality of Kodiak red king crabs.



measurement error because post-recruit abundance did not increase correspondingly the following year.

The estimates of legal crab abundance for Kodiak are compared with the mark-recapture estimates of Blau (1985) in Fig. 4. Blau's mark-recapture estimates tend to be somewhat lower in 1973–1978 and higher in 1980–1984. Higher mark-recapture estimates during the latter period correspond to years of reduced tag-recovery programs. Declining stocks also provided added incentives to some fishers who retained large numbers of tags to increase apparent stock size from Petersen estimation methods. The lower abundance estimates of CSA are associated with higher estimates of harvest rates than were estimated at the time of the fishery. Harvest rates increased until 1982 when the fishery collapsed; it has been closed since 1983 due to extremely depressed stock size.

The residuals of the CSA had a larger standard deviation for Bristol Bay than for Kodiak (Table 1). The recruit and post-recruit residuals for a given year tended to be positively correlated, as might be expected because they came from the same survey and the total survey catch was subject to a common measurement error. However, neither correlation was significant. The first-order autocorrelation of each residual time series was significant ($p = 0.05$) only for the Bristol Bay recruit residuals. This fit had a temporal pattern in the residuals attributable to the apparent shift in M (Fig. 1). Otherwise there

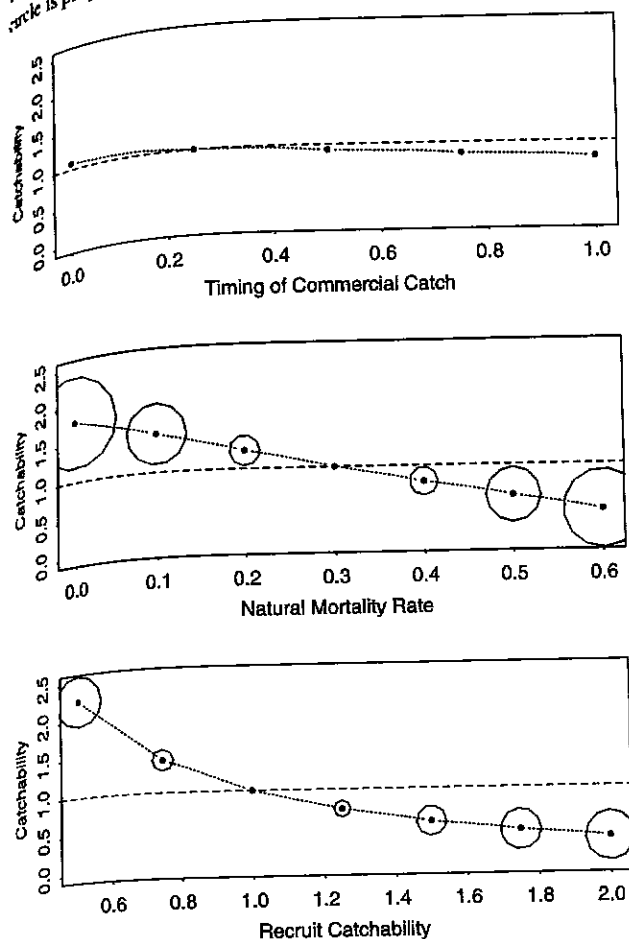
were no apparent patterns in the residuals that would indicate a violation of the model assumptions.

Sensitivity to errors in input data

Results are expressed as the deviation of q from its known value of 1.0 with errors in the input parameters (Fig. 5). The goodness-of-fit is indicated by the circles, the area of which is proportional to SSQ. With correct values of the input parameters and no errors in the relative abundance data, $SSQ = 0$. The estimate of q is insensitive to errors in specifying the timing of the commercial catch. Even though we specify an accurate annual value, the consequence of not doing so is minor. Likewise, discretizing a continuous catch would not be a problem. In this example T was constant at 0.25; increasing or decreasing the input T did not affect the sum of squares because e^{-MT} is a constant multiplier of q in eq. 3.

The q estimate is negatively correlated with M because the decline in numbers can be attributed to the commercial catch or natural mortality. Likewise, it can be seen from (eq. 3) that if we assume recruit mortality equals post-recruit mortality, when in fact the former is higher, q would be overestimated. The estimated q is also negatively correlated with recruit catchability (ϕ). For M and especially for ϕ , we must substantially deviate from the known input value to appreciably increase the sum of squares. The sum of squares of the fit to the actual data

Fig. 5. Sensitivity of the estimated catchability coefficient to errors specifying the input values of T , M , and ϕ in eq. 3. The correct values were $q = 1$, $T = 0.25$, $M = 0.3$, and $\phi = 1$. The area of each circle is proportional to the sum of squared residuals of the fit.



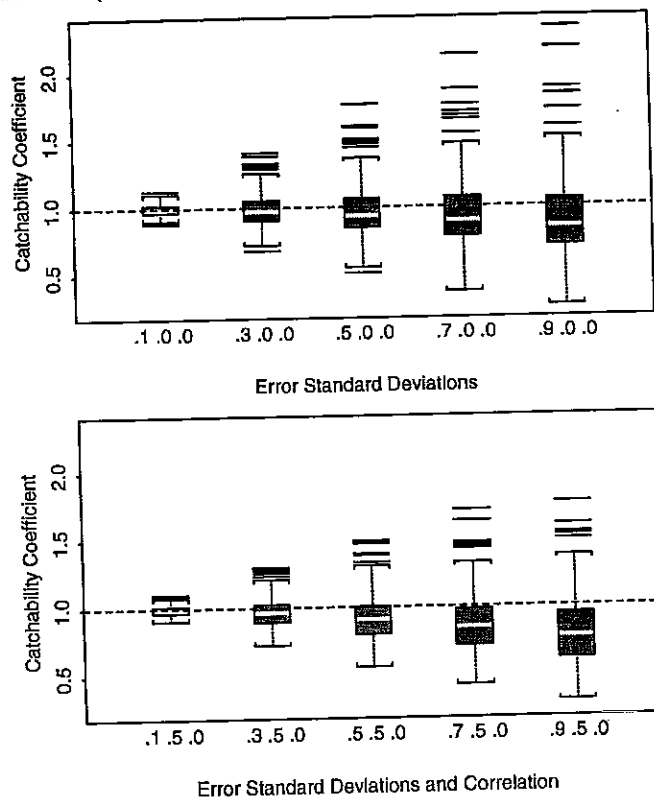
was more than twice as big as the largest circle in Fig. 5. It is therefore unlikely that we can estimate M or ϕ from real data sets in addition to q . These parameters are not structurally confounded in eq. 3, but their estimates will be strongly negatively correlated.

The simulated shell aging errors caused q to be slightly overestimated ($q = 1.01$, $SSQ = 0.007$). The sum of squared residuals between the CSA estimates and the original correct data was <0.001 , which indicates that CSA tends to correct for the aging errors. The simulated errors had little effect because the misclassification rates were small and symmetric. The bias in q would be larger if the aging errors were larger and there was a difference in magnitude between recruits and post-recruits, or if the aging errors were asymmetric.

Monte Carlo simulations

Box plots summarize the distributions of the q estimates relative to the true value of 1.0 (Figs. 6 and 7). A quantile plot of the log-transformed q estimates against the quantiles of the normal distribution (not shown) indicated that the distribution of estimated q 's was lognormal. Increasing the measurement-

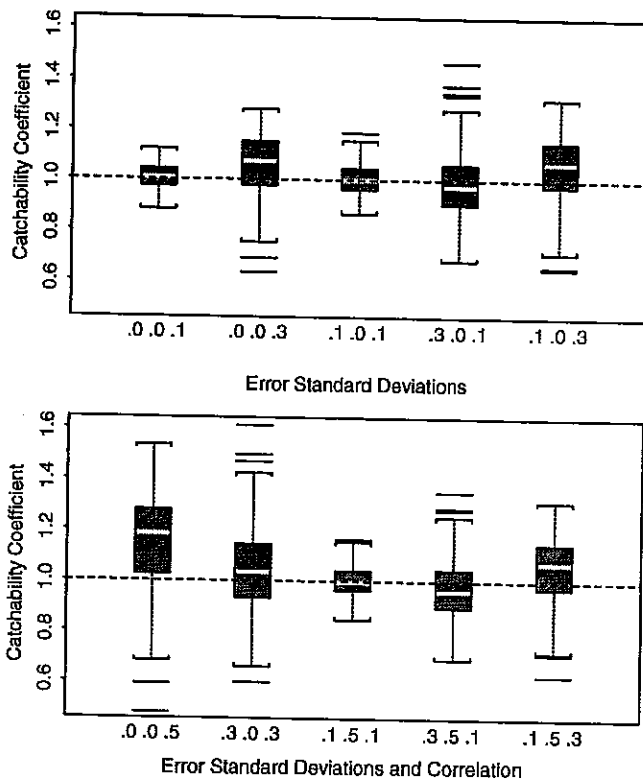
Fig. 6. Distributions of the catchability coefficients estimated in Monte Carlo simulations of catch-survey analysis. Each box plot summarizes the distribution of 200 q values. The white bar in the interior of the box is the median. The height of the box is equal to the interquartile distance (IQD). The whiskers extend $1.5 \times$ the IQD, or to the extreme range of the data, whichever is less. Individual lines beyond the whiskers are outliers. The three numbers under each box indicate the standard deviation of measurement errors, the correlation of measurement errors, and process error standard deviation (from left to right).



error standard deviation caused the distribution to be skewed downward and to have greater dispersion. The boxes in the bottom panel of Fig. 6 correspond to the ones in the top panel, with the addition of correlated measurement errors. With correlated measurement error the bias was greater and the dispersion less. The two real data sets had error standard deviations of 0.3 and 0.5; observed correlation in the residuals was low (Table 1).

Measurement and process errors caused different patterns in the simulated abundance data. With measurement errors, the distribution of post-recruit abundance fluctuated around the true values. With process errors, simulated abundance remained above or below the true abundance for extended periods, and was only tied to the true values because the correct recruitment was input each year. We therefore expected CSA to have more trouble reconstructing the true abundance with process errors, especially with an all measurement-error assumption. As the standard deviation of process errors was increased, the distribution of q was skewed upward (Fig. 7). At a standard deviation of 0.5, the dispersion was such that convergence difficulties were encountered. With mixed errors the negative bias from the measurement errors to some extent

Fig. 7. Distribution of the catchability coefficients estimated in Monte Carlo simulations of catch-survey analysis with mixed errors. The explanation of box plots is the same as for Fig. 6.



counteracted the positive bias from the process errors. Adding correlated measurement errors shifted the medians downward as in Fig. 6. The real data probably corresponded most closely to the cases in the upper right of Fig. 7.

Although it is convenient to express the simulation results with distributions of q , we are ultimately more interested in the distribution of absolute abundance estimates. Table 2 lists the average percent bias and coefficient of variation of legal abundance for combinations of measurement and process errors. With only measurement errors, the bias was low and the CV increased with the standard deviation. Process errors resulted in an increasingly negative bias, because q was overestimated. With mixed errors the bias was less than 5%. Simulated aging errors increased the bias and decreased the dispersion of the parameter estimates. The real data probably correspond most closely to the mixed-error simulations.

A parametric bootstrap was used to calculate the bias and dispersion of abundance estimates in each year for Bristol Bay and Kodiak red king crabs. The bootstrap standard errors of q were lower than those based on the asymptotic normality of the least-squares estimator (Table 1). We consider the bootstrap estimates to be more reliable because they are consistent with the Monte Carlo simulations with σ in the range 0.3–0.5. The bootstrap mean abundances were very close to the initial CSA estimates (Fig. 8), which indicates very small bias in the estimates. The empirical 95% confidence limits were quite symmetric and corresponded closely to ± 2 times the bootstrap standard deviation of q . The parametric confidence interval, which is slightly simpler to calculate, may therefore be adequate, although the empirical confidence limit is generally preferred. The confidence intervals were narrowest from 1980 to 1982 because of the high harvest rates. Depletion estimators perform better when a stock is heavily exploited.

Discussion

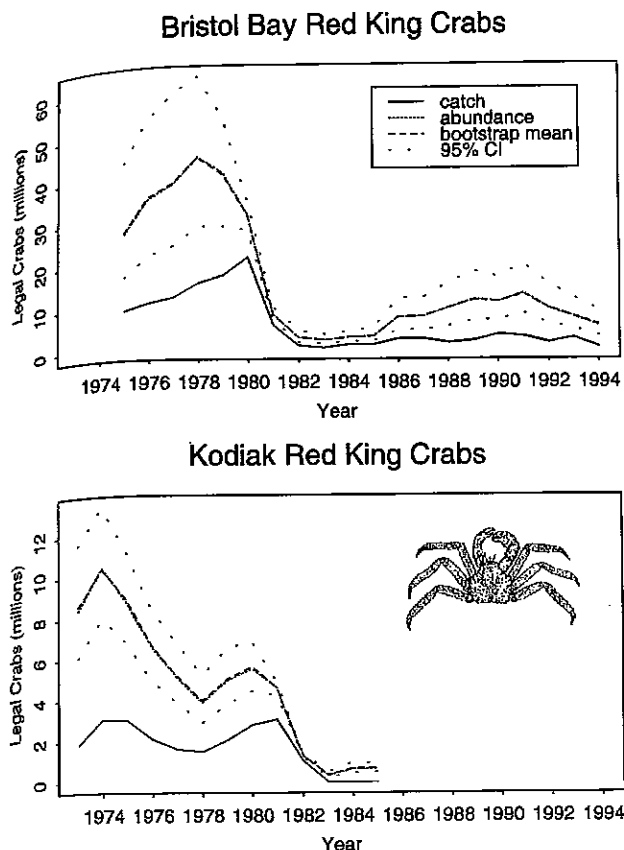
Catch survey analysis is useful for estimating the abundance of populations that can be classified into recruits and post-recruits

Table 2. Results of Monte Carlo simulations of catch-survey analysis.

Standard deviation of measurement errors	Correlation of measurement errors	Standard deviation of process errors	Proportion misaged	Bias of q estimates	Standard error of q estimates	Average % bias of abundance estimates	Average CV of abundance estimates	Number of replicates that converged
0.1	0.0	0.0	0.0	-0.00	0.04	0.2	5.1	200
0.5	0.0	0.0	0.0	-0.04	0.19	0.7	25.4	200
0.9	0.0	0.0	0.0	-0.10	0.31	-1.1	47.1	200
0.1	0.5	0.0	0.0	-0.01	0.04	0.30	4.8	200
0.5	0.5	0.0	0.0	-0.08	0.18	3.72	24.8	200
0.9	0.5	0.0	0.0	-0.20	0.27	7.16	48.3	196
0.0	0.0	0.1	0.0	0.01	0.05	0.0	12.0	200
0.0	0.0	0.3	0.0	0.06	0.13	-3.6	34.4	200
0.0	0.0	0.5	0.0	0.14	0.19	-11.6	54.3	192
0.1	0.0	0.1	0.0	0.00	0.06	0.1	12.9	200
0.3	0.0	0.1	0.0	-0.01	0.13	0.4	19.3	200
0.1	0.0	0.3	0.0	0.06	0.13	-3.0	34.5	194
0.3	0.0	0.3	0.0	0.04	0.17	-3.4	37.0	198
0.3	0.0	0.3	0.1	0.06	0.13	-5.7	31.3	200
0.3	0.5	0.3	0.1	0.04	0.14	-4.4	32.4	200

Note: The known data set was based on the Bristol Bay data set with $q = 1$. The averages are over the 20 years of the data set.

Fig. 8. Bootstrap abundance estimates of Bristol Bay and Kodiak red king crabs. The 95% confidence intervals (CI) are the 2.5 and 97.5 percentiles of 1000 bootstrap replicates.



and for which the commercial catch in numbers is recorded. It is particularly useful for stocks with limited age data, either because they cannot be aged or because of the expense of age determination. King crabs are excellent candidates for CSA because shell age can be used to classify them into recruits and post-recruits, even though the absolute age is unknown. For many other exploited fish and shellfish stocks a recruitment index can be obtained from the size-frequency distribution of survey data. Additional auxiliary information (e.g., commercial catch per unit effort) can be included in the estimation. The CSA framework can readily be customized for application to a wide range of populations (Conser 1991; Conser and Idoine 1992).

An advantage over direct area-swept estimates from trawl surveys is that CSA attempts to separate measurement errors from true changes in stock abundance, whereas area-swept estimation methods ignore information about the stock from prior years by implicitly assuming that each year's observation is completely independent. Another advantage is that CSA provides a method to estimate catchability of survey gear. This calibration is important for trawl surveys in which catchability is uncertain, and it is critical for pot surveys which would otherwise provide only an estimate of relative abundance.

In this study we extended the original CSA formulation

(Collie and Sissenwine 1983) by allowing for annual estimates of the timing of the commercial catch and natural mortality. More importantly, we rigorously tested the performance of the estimation method with known data sets and Monte Carlo simulation. The measurement-error model provided robust estimates of q and abundance. Of 3000 Monte Carlo trials reported in Table 2, only 20 (0.67%) failed to converge to a solution, and these failures were for high error levels unlikely to be encountered with real data sets. A mixed measurement- and process-error model may still be appropriate for larger data sets with relatively small measurement errors; the measurement-error model is a robust alternative when these conditions are not met.

The deviations in the median q values from the true value (Figs. 6 and 7) can be explained by the fact that the multiplicative lognormal errors, $\exp(\epsilon - \sigma^2/2)$, were scaled to have mean 1. The median of the errors is less than one and therefore the median q was either less than or greater than one, depending on the assumed error structure. The bias in the mean q values (Table 2) probably results from the propagation of the errors over time. With simulated measurement errors there was a negative bias in q , that increased with increasing error standard deviation (σ). Interestingly, the corresponding estimates of abundance were less biased than q (Table 2), perhaps because of covariance between the estimates of q and relative abundance.

Simulated process errors caused a positive bias in q (Table 2) which can be explained by the observation that, in many of the random data sets, the simulated post-recruits remained below the true abundance for most of the years. To account for the apparent greater mortality of post-recruits, the effect of the catch was increased and q overestimated. If real data sets contain high levels of process error ($\sigma \geq 0.5$), the positive bias in q and corresponding negative bias in abundance (Table 2) would be of concern. Whether an alternative error structure is desirable in this situation could only be determined with Monte Carlo simulation of a mixed-error estimation model with mixed-error data sets.

In simulation trials with mixed errors, the negative bias in q caused by the measurement errors tended to cancel the positive bias caused by process errors (Table 2). Correlated measurement errors and aging errors increased the bias of q and decreased the dispersion (Figs. 6 and 7). Both types of error accentuate deviations of the simulated data from the correct data. If recruit and post-recruit abundances are of the same magnitude and aging errors are symmetric, the 10% of recruits misclassified as post-recruits tends to be replaced by the 10% of post-recruits misclassified as recruits, with little net effect on the relative abundance estimates.

Turning to the real data sets for Bristol Bay and Kodiak, the error standard deviations (σ) of 0.3 and 0.5 are probably partitioned between measurement and process errors, though the exact ratio is unknown. The various error combinations with $\sigma = 0.1, 0.3$, or 0.5 probably bracket the true error variances. Correlation of the residuals from the observed data sets was low (Table 1), and even a correlation of 0.5 had a minor effect on parameter estimation. We consider the aging errors represented by eq. 7 to be conservative estimates because the reclassification was done by different people with less training at a later date. Shell age misclassification appears to be a minor

source of error in estimating the abundance of these king crab stocks. Considering the most likely magnitudes of all the potential sources of error, we conclude that the biases will in most cases be acceptable (<5%) and in many cases negligible. Correcting the abundance estimates for bias is inadvisable because the direction of the bias depends on the source of the errors, which is unknown in real data sets. Even with the shorter Kodiak data set (13 yr), the precision of the abundance estimates was acceptable (Fig. 8). The CSA performed well because both stocks were depleted in the early 1980's. Lower precision is expected for shorter time series and stocks that have been less heavily exploited.

Both red king crab stocks underwent major changes. In Bristol Bay, abundance of legal males increased during the late 1970's, declined sharply in the early 1980's, increased slightly in the late 1980's, and declined since then (Fig. 2). For Kodiak, legal abundance generally declined by 1 million crabs per year in 1973–1985 with the exception of a slight increase during the late 1970's (Fig. 4). These absolute abundance estimates are consistent with estimates obtained with mark-recapture studies (Blau 1985), area-swept calculations (Otto 1986), and length-based analysis (Zheng et al. 1995). This correspondence is partly due to our choice of $M = 0.36$, but even with the M value commonly used by the North Pacific Fishery Management Council (0.3) our absolute abundance estimates would be only slightly lower. This cross-validation of abundance estimators supports the use of CSA for stocks, such as those in Southeast Alaska, where no other absolute abundance estimates are available (Woodby 1994).

What caused the decline of these red king crab populations? Although the primary purpose of our study was to test the sensitivity of CSA to various errors and model assumptions, our results provide some insight into this difficult question. Comparison of abundance and catch partly implicates the fishery in the declines (Figs. 2 and 4). In both cases, harvest rates <40% generally corresponded to periods of relatively stable or increasing abundance, whereas harvests >40% were associated with periods of stock decline. Moreover, the highest harvest rates (>50% for Bristol Bay and >80% for Kodiak) coincided with the sharpest declines in the early 1980's. However, fishing does not fully explain stock changes. A sharp increase in apparent natural mortality during the early 1980's contributed to the collapse in Bristol Bay (Fig. 2).

Our analysis of the potential effects of temperature on M produced mixed results for Kodiak and Bristol Bay. The potential role of temperature deserves further study, because the effects could be more complex (e.g., nonlinear relationships and time lags) than we modeled. Otto (1986) speculated that Pacific cod (*Gadus macrocephalus*), a major predator of red king crabs, could have a substantial effect on crab mortality. To explore this, we ran additional CSA trials using age 3–12 cod abundances for the Gulf of Alaska (Thompson and Zenger 1994) and Bering Sea (Thompson 1994). For Bristol Bay, the fit was improved ($q = 1.05$, $SSQ = 3.326$) but for Kodiak the fit was worse than with constant M ($q = 1.09$, $SSQ = 1.175$). Livingston (1989) estimated that cod ate only a small percentage (1.4–3.8%) of the red king crab stock in the Eastern Bering Sea during sampling years 1981, 1984, and 1985; she concluded that cod were not a major cause of the red king crab decline in the early 1980's.

Low recruitment in the early 1980's also contributed to the

collapse of both king crab stocks. The close relations between recruit (Figs. 1 and 3) and legal male abundances (Figs. 2 and 4) show that both populations are largely driven by recruitment variations. The lack of recovery of the Bristol Bay stock since the early 1980's has been attributed to low spawning biomass (Zheng et al. 1995). These authors estimated two stock-recruitment relationships for Bristol Bay that provide competing interpretations of recruitment trends: a dome-shaped curve stresses the importance of density-dependent effects, whereas a curve that is flat over intermediate to high levels of spawning biomass emphasizes autocorrelated environmental effects. The fact that these two relationships fit the data equally well illustrates the classic problem of separating stock and environmental effects on recruitment. Armstrong (1983) speculated that year-class strength of red king crabs was determined by a suite of biotic and abiotic factors affecting reproductive success, larval survival, and survival of young juveniles and that the fishery could exacerbate these effects. Attempts to better understand this recruitment process are ongoing (Tyler and Kruse 1995).

New developments for application to red king crabs could include a three-stage model. Because molting probability is nearly unity until legal size is attained, the extension of our model to include a third stage, pre-recruits, is possible. This development would incorporate the mature but sublegal male component of the population which is part of the harvest strategy of Bristol Bay red king crabs. A three-stage model would be intermediate between the two-stage catch-survey analysis and a full length-based analysis.

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