Updated Length-Based Population Model and Stock-Recruitment Relationships for Red King Crab in Bristol Bay, Alaska

J. Zheng, M. C. Murphy, and G. H. Kruse

Reprinted from the
Alaska Fishery Research Bulletin
Vol. 2 No. 2, Winter 1995

Alaska Fishery Research Bulletin 2(2):114–124. 1995.

Updated Length-Based Population Model and Stock-Recruitment Relationships for Red King Crab in Bristol Bay, Alaska

J. Zheng, M. C. Murphy, and G. H. Kruse

ABSTRACT: A length-based population model for Bristol Bay red king crab *Paralithodes camtschaticus* was updated and applied to abundance and catch data from 1968 to 1994. The updated model has fewer parameters and assumes constant natural mortality over length and 2 levels of natural mortality over time for males and 3 levels for females. A nonlinear least squares approach was used to estimate abundance, recruitment, and natural mortality. We added confidence intervals for the abundance estimates with a bootstrap percentile method. Natural mortality was estimated to be 4 to 5 times higher in the early 1980s than during other periods. The observed population abundances were well fitted by the updated model. Confidence intervals for legal male abundance were narrower than for mature female abundance. The stock-recruitment data estimated from the updated length-based model provided a good fit to both general and autocorrelated Ricker models. However, recruitment estimates were lower and the relationships were slightly more depensatory than in the previous model.

INTRODUCTION

In a previous study Zheng et al. (1995) developed a length-based population model for Bristol Bay, Alaska red king crab (RKC) *Paralithodes camtschaticus* that incorporates stochastic growth, gradual recruitment over length, time-variable natural mortality, and a bowl-shaped curve of natural mortality over length. Parameters of the model were estimated using available trawl survey, fishery, and tagging data. The model fit the data well but some reviewers' concerns about overparameterization led us to reexamine the model structure and subsequently prepare the updated model described in this paper.

We revised our earlier work in several ways. First, we incorporated the most current data through 1994. Second, we made a number of improvements to the model that reduce the number of parameters to be estimated, thereby increasing the number of degrees of freedom (*df*). Towards this end, we (1) fixed natural mortality over length rather than attempting to estimate a length-specific mortality function, (2) reduced the number of temporal shifts in natural mortality to be estimated, (3) separated the male abundances by shell condition in the last length class instead of lumping them together, and (4) reduced the small constant used in the objective function to prevent underweighting of low abundances. The final improvement is that we used a bootstrap method to construct confidence intervals for the abundance estimates. The general and autocorrelated Ricker stock-recruitment (S-R) models were updated accordingly. The model continues to filter out measurement errors, which improves estimates of annual population abundance for setting a harvest quota.

METHODS

Data sources, model structure, parameter estimation, and S-R models are detailed in Zheng et al. (1995). Rather than separating natural mortality into length- and time-dependent components, the updated model simplifies the function for instantaneous natural mortality to a time-dependent component (M_t) that is constant over length. Also, rather than estimating 4 levels of natural mortality over time, 3 levels were estimated for females and 2 for males. Equations (8), (9), and (10) of Zheng et al. (1995) are now written as

$$N_{l+1,\,t+1} = \sum_{l'=1}^{l'=l+1} \{P_{l',\,l+1}[(N_{l',t} + O_{l',t})\,e^{-M_t} - C_{l',\,t}\,e^{(y-1)M_t}]\,m_{l',\,t}\} + R_{l+1,\,t+1}\text{, and} \qquad (1)$$

$$O_{l+1,\,t+1} = [(N_{l+1,\,t} + O_{l+1,\,t})\,e^{-M_t} - C_{l+1,\,t}\,e^{(y-1)M_t}]\,(1 - m_{l+1,\,t})\ ,$$

Authors: JIE ZHENG is a biometrician, MARGARET C. MURPHY is the statewide shellfish biometrician, and GORDON H. KRUSE is the marine fisheries scientist for the Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, P.O. Box 25526, Juneau, AK 99802-5526.

Acknowledgment: Robert S. Otto — suggested a need for revisions in the initial model.

Project Sponsorship: This paper was funded in part by cooperative agreement NA37FL0333 from the National Oceanic and Atmospheric Administration (NOAA). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

where

$N_{l,t}$ = new-shell crab abundances in length class *l* and year *t*,

$O_{l,t}$ = old-shell crab abundances in length class *l* and year *t*,

M_t = instantaneous natural mortality in year *t*,

$m_{l,t}$ = molting probability for length class *l* in year *t*,

$R_{l,t}$ = recruitment into length class *l* in year *t*,

y = lag in years between assessment survey and the fishery,

$P_{l',l}$ = proportion of molting crabs growing from length *l'* to length *l* after 1 molt, and

$C_{l,t}$ = catch of length class *l* in year *t*.

We set the minimum carapace length (CL) at 95 mm for males and 90 mm for females and modeled crab abundance using length-class intervals of 5 mm. The last length class included all crabs with lengths ≥169 mm for males and ≥140 mm for females. For a slightly better estimate of molting probability, the new-shell and old-shell males in the largest length class were separated instead of being lumped together, as in our previous model.

As before, parameters of the model were estimated using a nonlinear least squares approach, which minimized the residual sum of squares (*RSS*), or measurement errors. Equation (12) of Zheng et al. (1995) was rewritten as

$$RSS = \sum_{l,t} \{[\ln(N_{l,t} + \kappa) - \ln(\tilde{N}_{l,t} + \kappa)]^2 + [\ln(O_{l,t} + \kappa) - (\ln(\tilde{O}_{l,t} + \kappa)]^2\}, \qquad (2)$$

where $\tilde{N}_{l,t}$ and $\tilde{O}_{l,t}$ are estimated abundances of new-shell and old-shell crabs in length class *l* and year *t* from trawl survey data, and κ is a constant set equal to 100,000 crabs (instead of 500,000 crabs previously). Constant κ was used to prevent taking the logarithm of zero and to reduce the effect of length classes with zero or very low abundances on parameter estimation. A smaller κ gives a heavier weight for low abundances, and vice versa. Because recently observed abundances are low, we used a smaller κ to prevent underweighting. The total data points are 617 for males and 243 for females. Residuals between adjacent length classes and between years were examined to check the assumption of independence.

A bootstrap percentile method (Efron and Tibshirani 1993) was used to construct confidence intervals for abundance estimates. Because the absolute residuals for the old-shell males and large crabs were higher than new-shell males and small crabs, we structured residuals by sex, shell condition, and length class as year vectors and randomly sampled across years. The sampled vectors of residuals were added to the model-estimated abundances for a particular sex, shell condition, and length class but different years. We used 2,000 replicates to ensure stable estimates of confidence intervals (Efron and Tibshirani 1993).

RESULTS

Length-Based Population Model

Two levels of natural mortality over time were estimated for males (1972–1979/1985–1993; 1980–1984) and 3 levels for females (1972–1980; 1981–1984; 1985–1993). These levels appeared to fit the data quite well. The natural mortality was low in the 1970s (0.227 for males and 0.472 for females), dramatically increased in the early 1980s (1.039 for males and 1.722 for females), and then returned to low levels in the mid 1980s (0.227 for males and 0.317 for females; Table 1). As with the previous model, the estimated natural mortality was much higher for females than for males, and recruitment for both male and female crabs was very strong in the 1970s and extremely weak in recent years (Table 1).

Residuals for small females and small new-shell males were less dispersed than residuals for large females and large new-shell males (Figure 1), whereas old-shell males had the largest absolute residuals. For a given year, residuals within the same shell condition tended to have the same sign, especially for females and old-shell males (Figure 2). Residuals for adjacent length classes within shell conditions and years were significantly correlated (r = 0.754 and df = 572 for males and r = 0.789 and df = 220 for females), but the annual means of absolute residuals were not strongly associated between years (r = 0.435 and df = 21 for males and r = 0.315 and df = 21 for females). In general, the distributions of residuals for both males and females appeared to be symmetric with medians close to zero (Figures 1, 2).

The model closely fit the observed abundance by length, shell condition, and sex (Figures 3, 4). It appeared to overestimate the old-shell male crabs in 1974, 1980, 1985, and 1988. The abundance of new-shell males was much higher than the old-shell males, except in recent years when the legal male abundances of both shell conditions were similar.

Table 1. Parameter estimates for a length-based population model of red king crab in Bristol Bay. Recruits, R_t, are in millions of crabs and effective spawning biomass, SP_t, in thousand tonnes.

Parameter	Males	Females	Year	SP_t
N_{72}	39.176	59.498	1968	30.409
β	0.519	0.931	1969	33.091
β_r	1.885	0.313	1970	23.369
α_1	358930.100	NA	1971	24.462
α_2	20584.940	NA	1972	25.555
α_3	295159.600	NA	1973	30.032
β_1	0.082	NA	1974	44.627
β_2	0.077	NA	1975	52.820
β_3	0.089	NA	1976	58.744
M_{72}-M_{79}, M_{85}-M_{93}	0.227	NA	1977	79.472
M_{80}-M_{84}	1.039	NA	1978	89.969
M_{72}-M_{80}	NA	0.472	1979	75.348
M_{81}-M_{84}	NA	1.722	1980	75.154
M_{85}-M_{93}	NA	0.317	1981	27.446
R_{73}	33.721	32.845	1982	11.539
R_{74}	22.088	27.940	1983	7.682
R_{75}	34.126	21.819	1984	7.787
R_{76}	49.845	34.563	1985	4.995
R_{77}	67.574	71.262	1986	6.676
R_{78}	23.881	45.724	1987	11.269
R_{79}	12.816	18.689	1988	12.996
R_{80}	24.927	35.676	1989	14.288
R_{81}	17.578	13.387	1990	12.280
R_{82}	23.912	17.271	1991	12.274
R_{83}	12.989	4.828	1992	11.943
R_{84}	18.695	12.158	1993	10.782
R_{85}	11.164	4.901	1994	8.841
R_{86}	6.874	3.929		
R_{87}	7.264	9.053		
R_{88}	6.785	5.726		
R_{89}	5.653	5.634		
R_{90}	1.528	0.888		
R_{91}	4.035	3.723		
R_{92}	6.493	3.254		
R_{93}	2.580	1.869		
R_{94}	1.194	0.353		
RSS	108.547	34.167		
df	584	215		

For Bristol Bay, legal RKCs are defined as males ≥6.5 in carapace width (≥135 mm CL). The legal crab abundance increased dramatically in the middle and late 1970s and decreased precipitously in the early 1980s (Figure 5). After a moderate increase in the late 1980s, the legal crab abundance resumed the downward trend in recent years. Because there are several length classes modeled before legal crabs, measurement errors for legal crabs were mostly filtered out by multiyear data. Thus, 95% confidence intervals are very narrow for legal males (Figure 5).

Table 2. Parameter estimates of Ricker stock-recruitment models, equations (15) and (16) of Zheng et al. (1995), for Bristol Bay red king crab. Spawning stock is measured by the effective spawning biomass in tonnes. Recruitment is measured by male recruits, female recruits, or total male and female recruits combined at age 6.2 in thousands (i.e., 7-year time lag). Degrees of freedom are 16.

	General Model			Autocorrelation Model		
	Male	Female	Total	Male	Female	Total
r1	2.0437	2.6642	2.3319	NA	NA	NA
r2	-9.4812	-15.1362	-11.4026	0.0951	-0.2623	0.5234
r3	5.39e-5	7.80e-5	6.49e-5	1.99e-5	2.20e-5	2.05e-5
a1	NA	NA	NA	0.6000	0.5450	0.5933
R^2	0.56	0.60	0.59	0.61	0.56	0.60
σ	0.68	0.77	0.70	0.63	0.82	0.69

As with legal males, large (>89 mm CL) female abundance increased to a peak in the late 1970s, decreased dramatically in the early 1980s, and remained at low levels from the early 1980s through 1994 (Figure 6). Confidence intervals for large female abundance (Figure 6) are much larger than those for legal males (Figure 5), primarily due to (1) a smaller number of length classes modeled for females, such that few multiyear data are available to filter out measurement errors, and (2) a lack of information to refine estimates for females, such as catch and shell condition data used for legal males. The standard errors of observed abundances for females are also much larger on a year-to-year basis than for males.

With the addition of 1994 data, we were better able to estimate molting probabilities in recent years. Three levels of molting probabilities were estimated for male crabs: 1972–1979, 1980–1984/1992–1993, and 1985–1991. Molting probabilities were very high during 1972–1979, low during 1980–1984/1992–1993, and intermediate during 1985–1991 (Figure 7). Low molting probability tended to occur when the population abundance was declining.

The proportions of recruits by length are similar to those in our previous model. Recruitment to the model occurred in the first 8 length classes for males, 86% in the first 5 length classes (Figure 7). Female recruitment to the model occurred in the first 6 length classes, 95% in the first 3 length classes (Figure 7). The gamma distribution for proportions of recruits over length was truncated because crabs with sizes smaller than the first length class were not modeled. Thus, the total recruitment estimated was only an approximation of year-class strength.

Stock-Recruitment Model

Similar to our previous results (Zheng et al. 1995), a shortage of mature male crabs occurred in 4 years: 1972, 1973, 1981, and 1982. Thus, the effective spawning biomass during these 4 years was set equal to the biomass of the hypothesized maximum number of female crabs that can be fertilized by the males available, which was 9–33% less than the corresponding mature female biomass.

S-R relationships (Figure 8) closely resemble the previous results (Zheng et al. 1995). The general Ricker model (R^2 = 0.59, *df* = 16) fit the data almost as well as the autocorrelated Ricker model (R^2 = 0.60, *df* = 16; Table 2). All R^2 values are slightly lower than those from the previous model. Productivity parameter *r2* of the S-R curve is smaller and depensatory parameter *r3* is larger under the current model than under the previous model, but the overall shape of the S-R curve is similar.

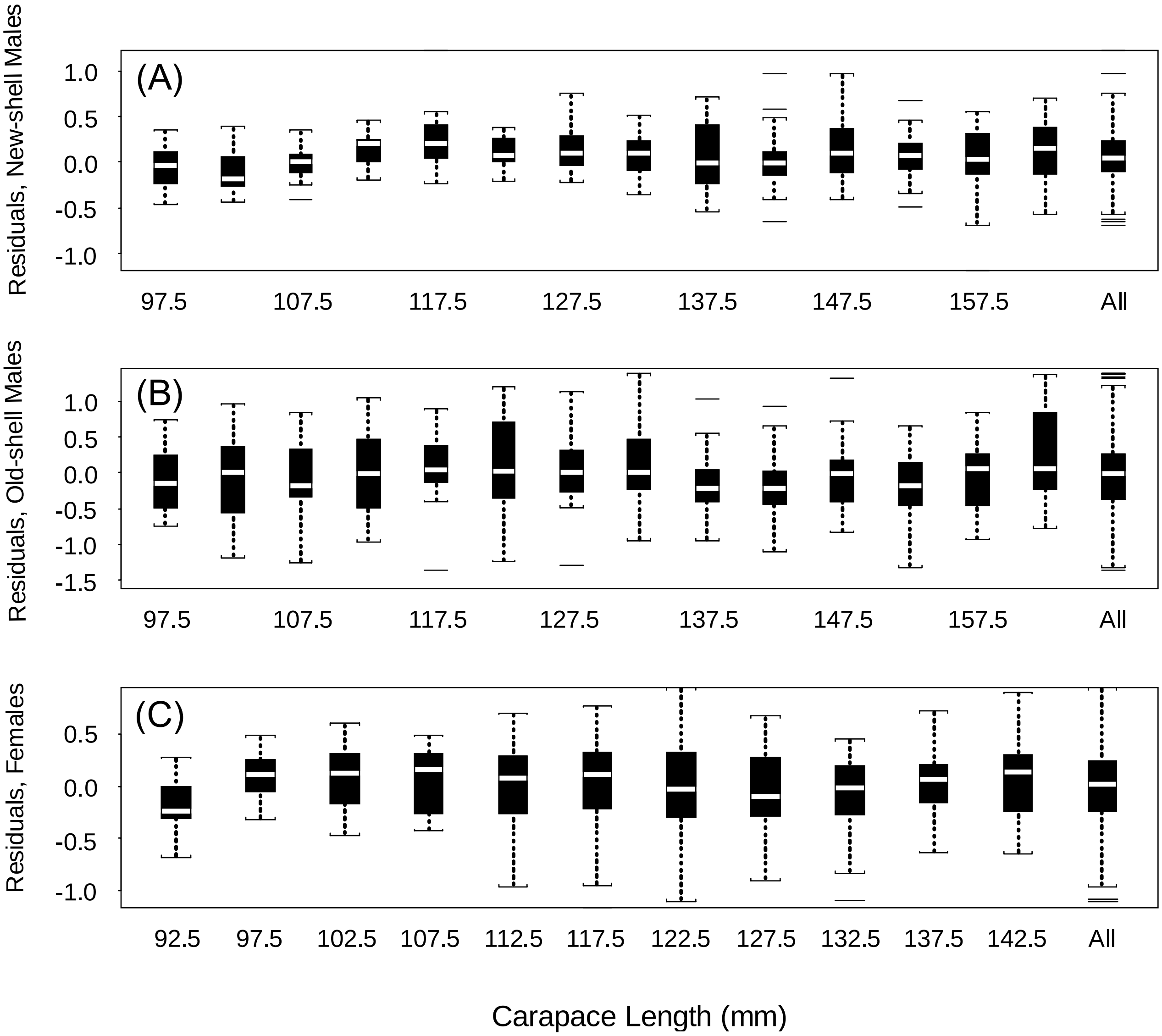

Figure 1. Box plots of red king crab residuals by length class for new- (A) and old-shell (B) males and females (C) in Bristol Bay. The white lines within shaded boxes are medians, and shaded boxes represent distributions of the central 50% of the data points. The full distribution of residuals is bounded by brackets and individual extreme residuals are depicted by single horizontal lines.

DISCUSSION

The main difference between the current length-based model and previous model (Zheng et al. 1995) is the structure of natural mortality. Because of confounding effects between recruitment and natural mortality as a function of length, we assumed constant natural mortality over length in the current model instead of the bowl-shaped curve used in the previous model. We also reduced the previous 4 levels (both sexes) of natural mortality over time to 2 levels for males and 3 levels for females. Thus, total number of parameters used to model natural mortality was reduced from 7 to 2 for males and to 3 for females. Given the available data, we might have overparameterized natural mortality in the previous model. However, regardless of the particular assumption, it is clear that Bristol Bay RKC experienced a pronounced shift to high natural mortality during the early 1980s. Contributing factors to this high natural mortality may include environmental change, disease, predation, bycatch, and handling mortality.

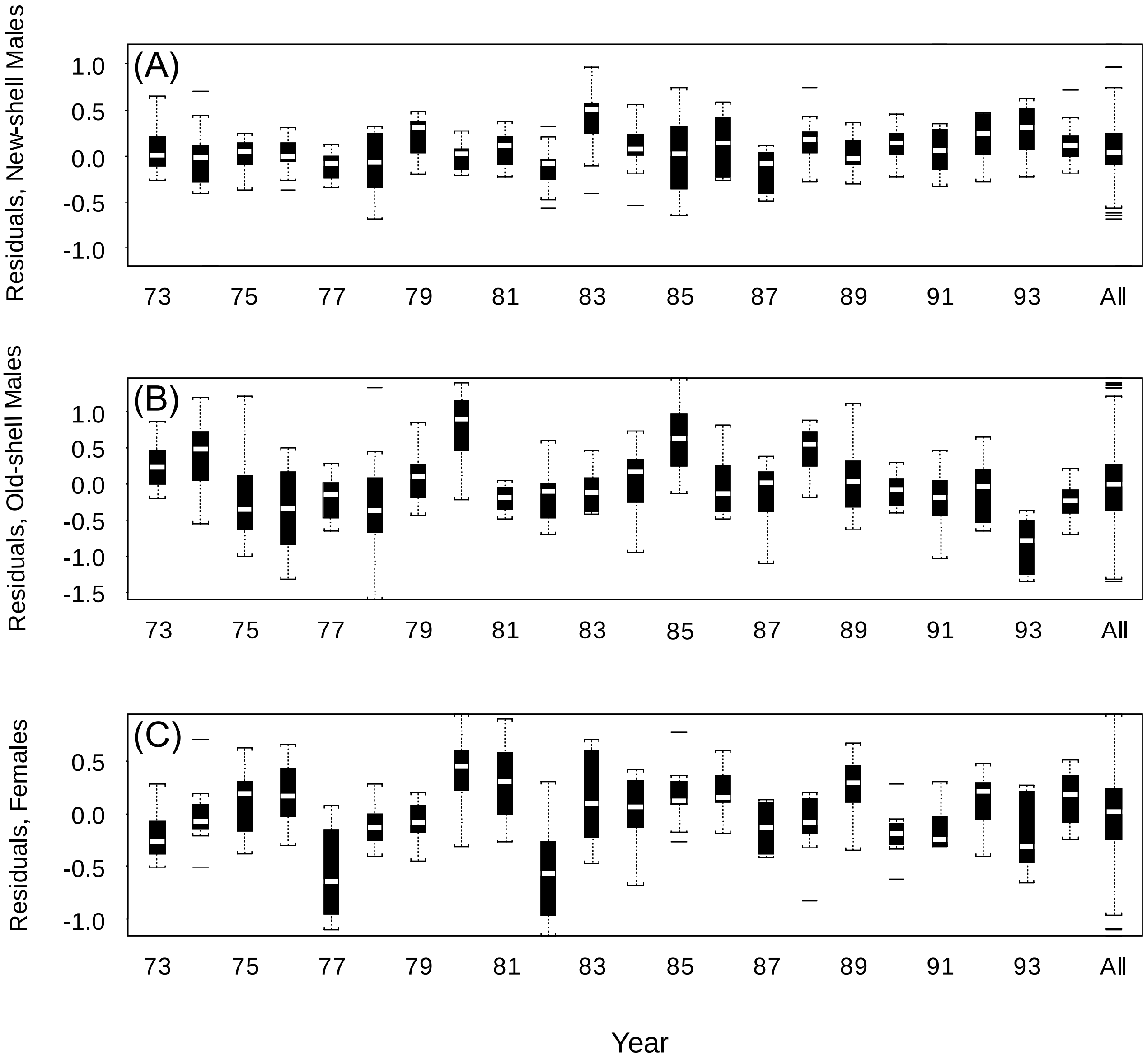

Figure 2. Box plots of red king crab residuals by year for new- (A) and old-shell (B) males and females in Bristol Bay. The white lines within shaded boxes are medians, and shaded boxes represent distributions of the central 50% of the data points. The full distribution of residuals is bounded by brackets and individual extreme residuals are depicted by single horizontal lines.

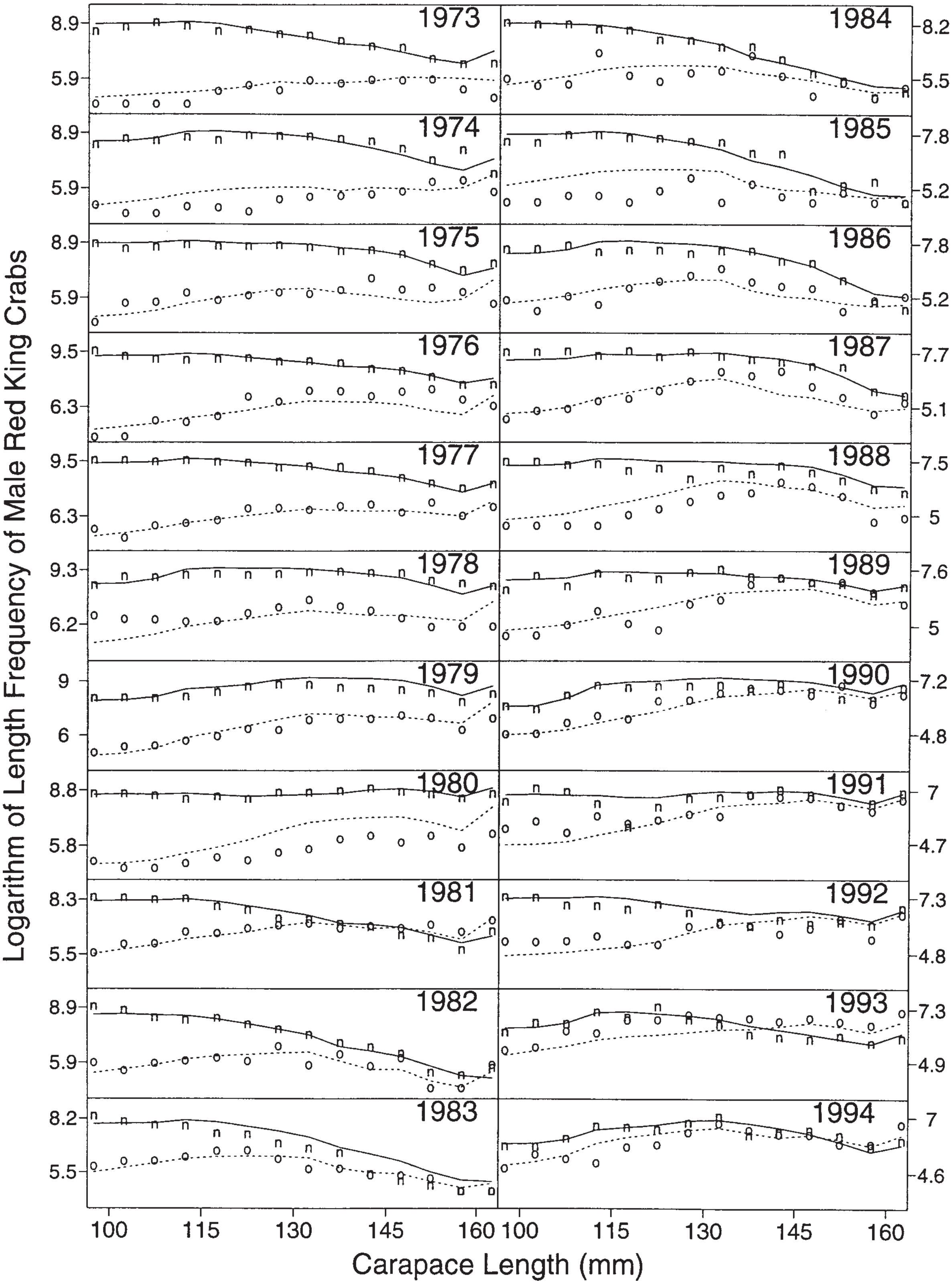

Figure 3. Comparison of observed (letters *n* for new-shell and *o* for old-shell) and estimated (solid line for new-shell and dotted line for old-shell) logarithm of length frequencies of Bristol Bay male red king crabs by year (1973–1994).

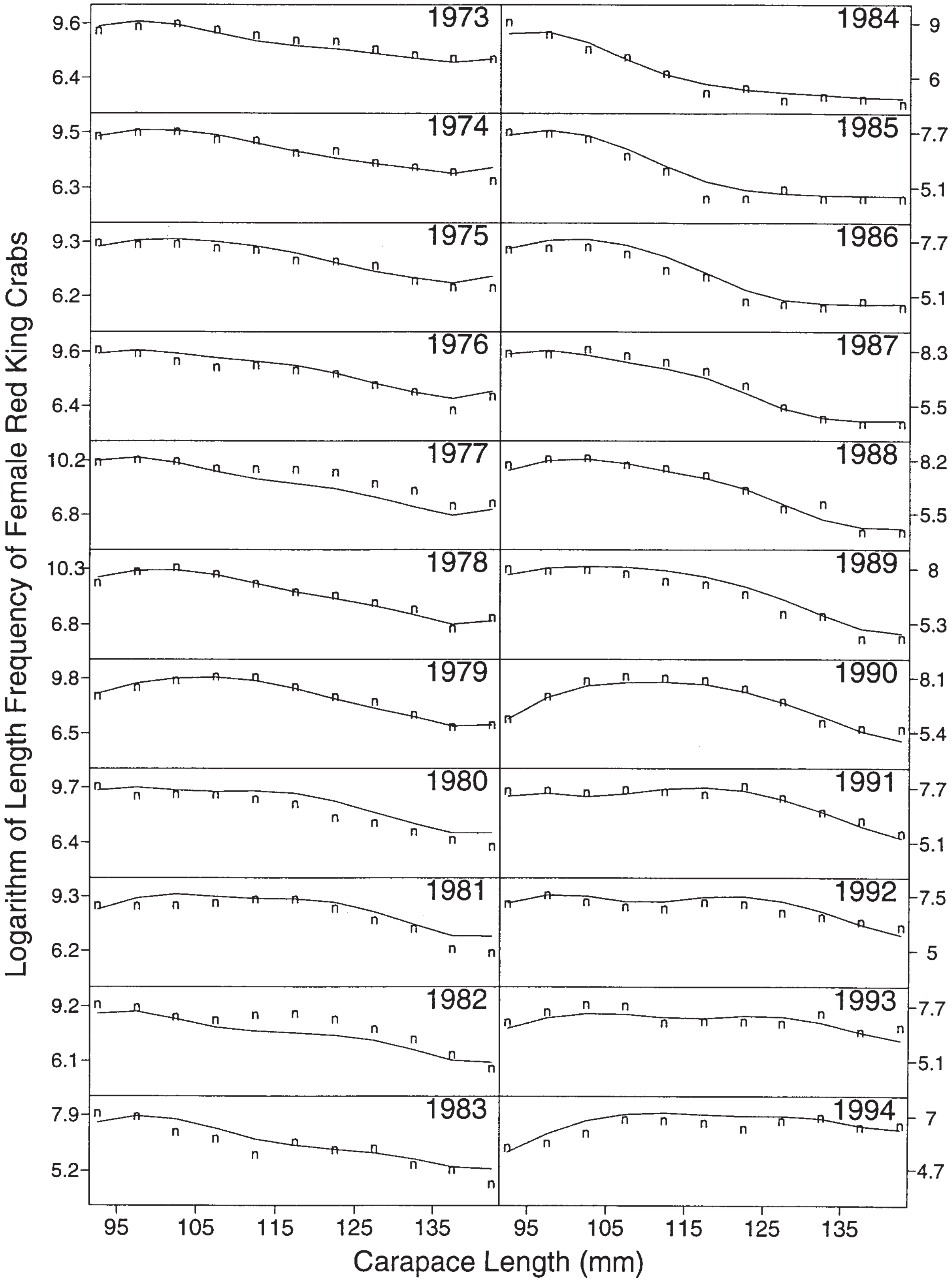

Figure 4. Comparison of observed (*n*) and estimated (solid line) logarithm of length frequencies of Bristol Bay female red king crabs by year (1973–1994).

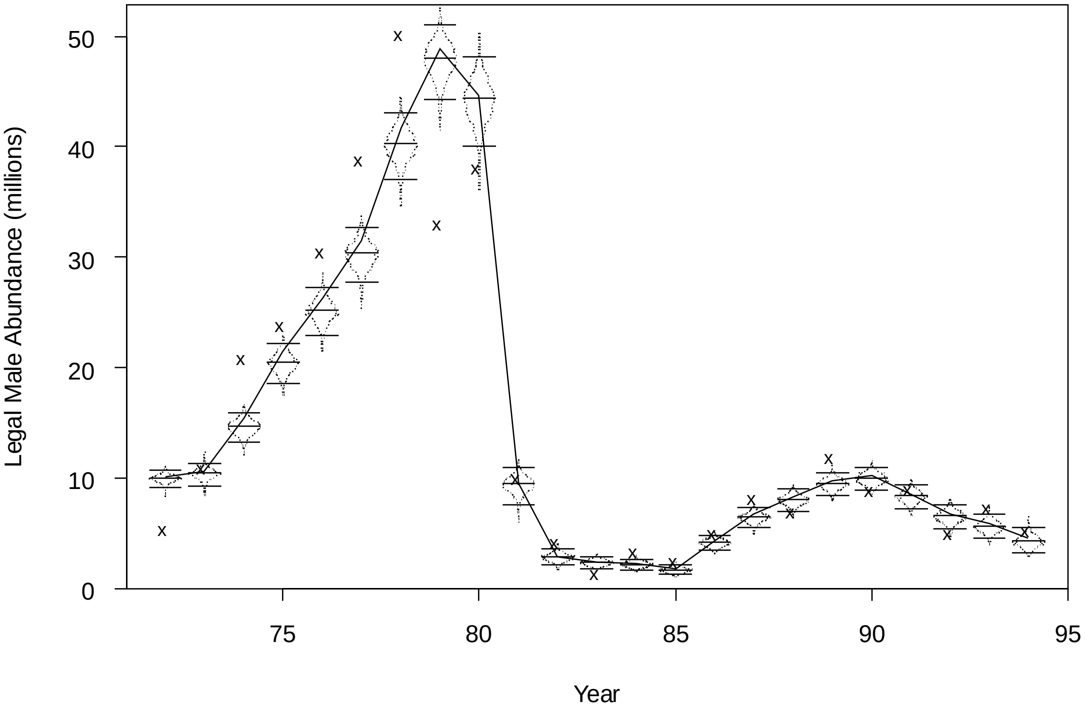

Figure 5. Comparison of observed (*X*) and estimated (solid line) legal male red king crab abundances in Bristol Bay and the estimated empirical (bootstrap) probability distribution (bell-shaped dotted lines). The 3 short parallel lines for each year are the median and 95% confidence intervals.

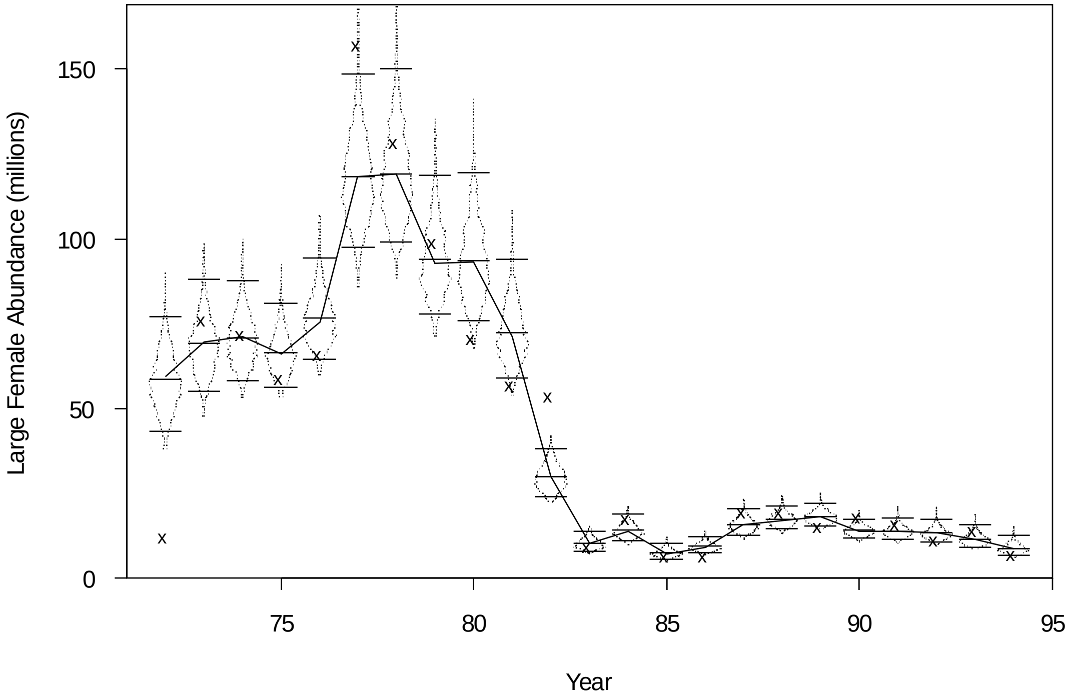

Figure 6. Comparison of observed (*X*) and estimated (solid line) large (CL >89 mm) female red king crab abundances in Bristol Bay and the estimated empirical (bootstrap) probability distribution (bell-shaped dotted lines). The 3 short parallel lines for each year are the median and 95% confidence intervals.

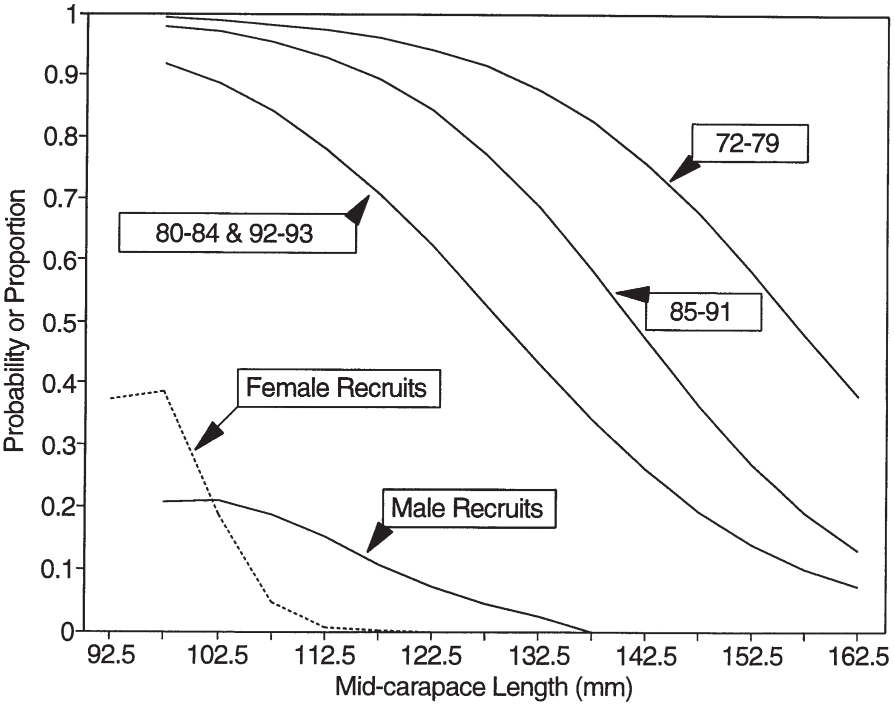

Figure 7. Comparison of estimated probabilities of molting of male red king crabs in Bristol Bay for different periods (1972–1979, 1985–1991, and 1980–1984/1992–1993) and proportions of recruits by length for male and female crabs.

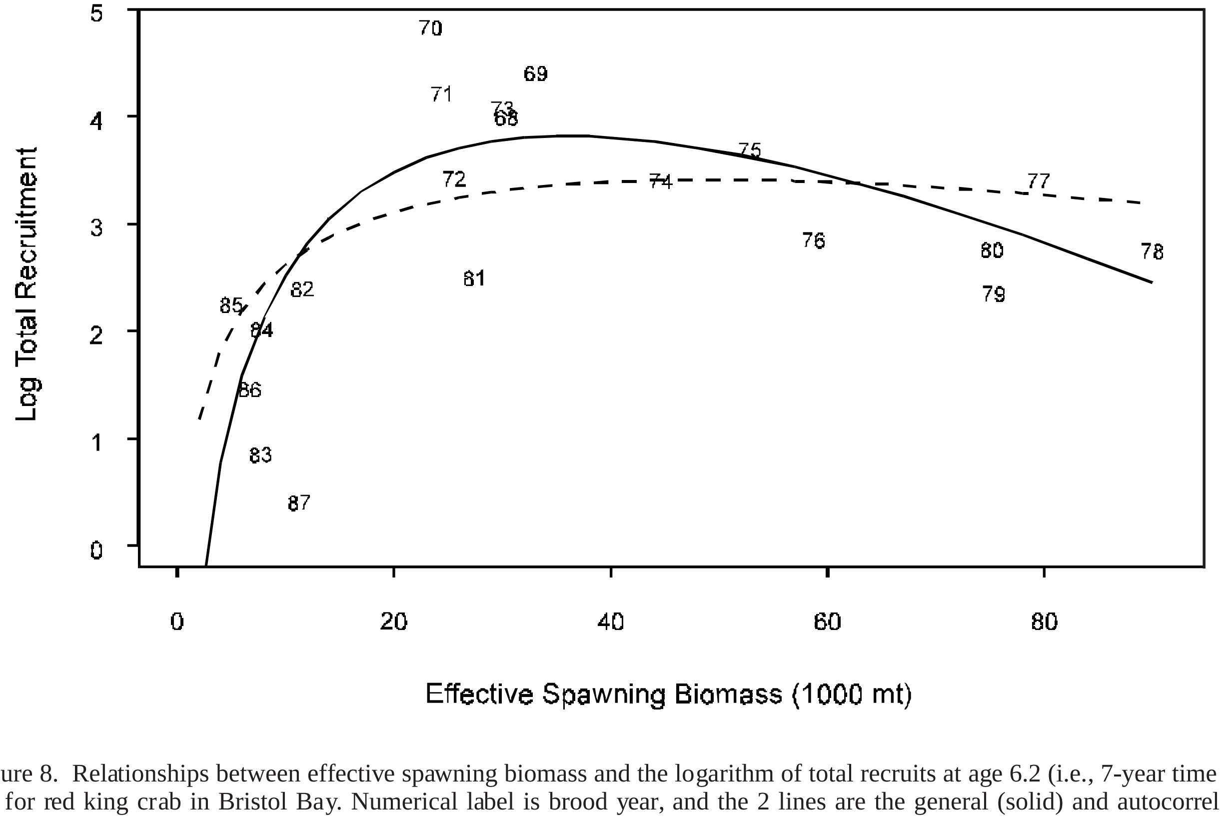

Figure 8. Relationships between effective spawning biomass and the logarithm of total recruits at age 6.2 (i.e., 7-year time lag) for red king crab in Bristol Bay. Numerical label is brood year, and the 2 lines are the general (solid) and autocorrelated (dotted) Ricker curves.

Other small modifications had minimal effects on the model. Addition of the 1994 data resulted in the best fit when the molting probabilities in 1992 and 1993 were grouped with the period from 1980 to 1984. This produced a slightly better fit than the previous model. The estimated abundances were insensitive to the reduction in κ and should remain so as long as κ is not extremely small or large relative to the observed abundances.

Although estimated abundances are similar between the current and previous models (Figure 9), some parameter estimates differ slightly. Estimated recruitment is generally smaller because the assumption of constant natural mortality over length reduces natural mortality for small crabs from the previous model. The difference between low and high natural mortality over time is smaller because of averaging that occurs when fewer levels of natural mortality are used. S-R relationships were slightly more depensatory than in the previous model. The more depensatory a S-R relationship is, the more prone the stock is to overfishing.

The bootstrap percentile method is one of the easiest approaches to construct confidence intervals of abundance estimates. Confidence intervals are approximated by taking the residuals from the best-fit model as estimates of true survey measurement errors and by sampling with a large number of replicates. Also, the empirical distribution of bootstrap abundance estimates can be used to assess the risk of a population being below *threshold* (i.e., a minimum spawning stock abundance or biomass below which fishing is prohibited), which will be helpful in making management decisions.

The percentile method may not provide satisfactory confidence intervals under some circumstances. For example, if the model parameter estimates are biased, the percentile intervals may not cover the true intervals very well. This problem can be partially overcome through a bias-corrected and accelerated method (Efron and Tibshirani 1993). However, it is difficult to apply this approach to a model as complex as our length-based analysis. Moreover, if absolute residuals

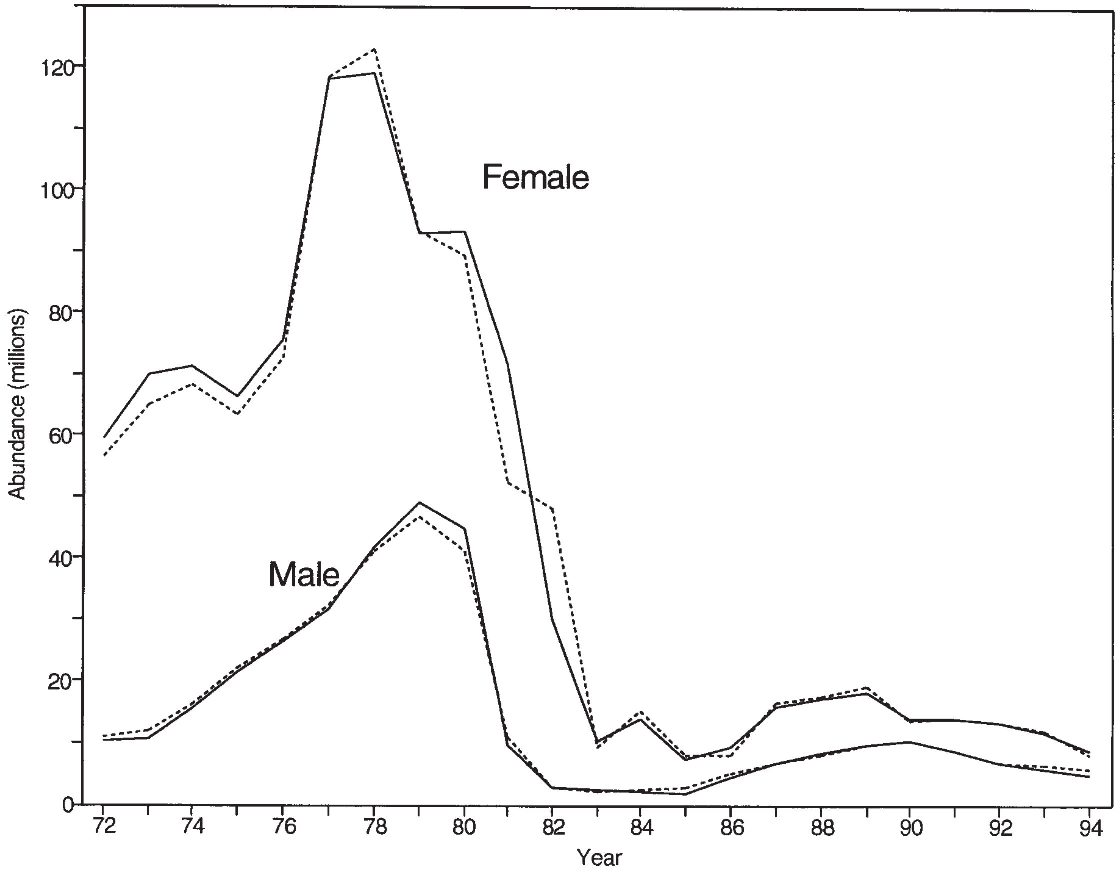

Figure 9. Comparison of estimated large (CL >89 mm) female and legal male red king crab abundances from the current model (solid line) and the previous (dotted line) model (Zheng et al. 1995) in Bristol Bay.

from the best-fit model are larger or smaller than the true survey measurement errors, the percentile method may over or underestimate confidence intervals of abundances accordingly.

The results from residual analysis indicate that measurement errors are likely to be lognormally distributed and independent between years, but not independent between length classes within a year. The means of residuals are about equal to zero, but the variance for old-shell males is larger than those for females and new-shell males. The variances for small females and new-shell males are the smallest. The large variance of residuals for old-shell males may be partially caused by modeling too few shifts in molting probability over time. Increasing the number of levels of molting probability over time will considerably reduce the variance for old-shell males but increase the number of parameters to be estimated and, thus, reduce the number of degrees of freedom. Other factors that affect measurement errors for old-shell crabs may include relatively small abundance, shell condition identification errors, and survey errors due to changes in catchability and distribution of old-shell males. Note that although residuals may be primarily due to measurement errors, process errors caused by model misspecification may also contribute to residuals. The small variance of residuals for small females and new-shell males may primarily result from estimating recruitment from these length classes. In other words, process errors may have somewhat increased the variance of residuals for old-shell males and decreased the variances for small females and new-shell males.

In constructing our model, we assumed that measurement errors were lognormally distributed and independent between years and among length classes within a year. We now know that this assumption is partially invalid. Myers and Cadigan (1995) reported that high correlation of measurement errors among age classes for a given year biases catch-at-age analysis of abundance estimates in recent years. Moreover, the correlation of residuals between adjacent length classes in a year will reduce the effective degrees of freedom below those presented in Table 1. However, this may not greatly affect parameter and abundance estimates in our model because our objectives are still to minimize measurement errors, and we primarily depend on survey data. Effects of different structures of measurement errors on parameter and abundance estimates under a length-based model should be evaluated in future studies.

In summary, the current model fits the observed data almost as well as the previous model. Nonetheless, we believe the model is better in a way not measured by residual sum of squares. The model is more parsimonious in that it estimates fewer parameters than the previous version. Our current assumptions of constant mortality over length and decadal-scale shifts in mortality over time seem prudent given the limitations of the data. In reality, however, it is likely that mortality varies annually and with the size of crabs. Undoubtedly, further model refinements will become necessary when new information becomes available. The parameter estimates need to be updated annually with new survey and fishery data to estimate population abundances used to set guideline harvest levels and assess the risk of the population being below threshold.

LITERATURE CITED

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, Inc., New York.

Myers, R. A., and N. G. Cadigan. 1995. Statistical analysis of catch-at-age data with correlated errors. Canadian Journal of Fisheries and Aquatic Sciences 52:1265–1273.

Zheng, J., M. C. Murphy, and G. H. Kruse. 1995. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 52:1229–1246.