

**Abstract.**—A catch-length model was constructed to estimate abundance of crab populations for which no survey data are available. The model incorporates stochastic growth by length and gradual recruitment over length and assumes constant catchability. Required data include catch by length and shell condition, fishing effort, growth increment per molt by length, and annual natural mortality rate. Model application to red king crab populations in Bristol Bay and off Kodiak Island, Alaska, generally provides accurate estimates of trends of relative population abundances. The accuracy of absolute abundance estimates depends on knowledge of natural mortality. The model provided a good fit to the catch by length and shell condition for both populations. In comparison to population abundances estimated directly from surveys, the catch-length model performed best with instantaneous natural mortality set equal to 0.4 and with fishing effort and catch-length/shell composition weighted equally in the calculation of residual sum of squares.

## A catch-length analysis for crab populations\*

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Molting is one of the most important biological differences between crabs and fishes. The hard structure of crabs is replaced during molting, which makes direct ageing of crabs extremely difficult. The molting process of an individual crab is short, normally a few days, resulting in punctuated growth. Molting frequency of red king crab (RKC, *Paralithodes camtschaticus*) depends on body size and varies over time (Balsiger, 1974). Thus, ability to age crabs indirectly by conventional length-frequency analysis is questionable. Without age information, a conventional catch-age analysis cannot be applied to crab populations.

An alternative to a catch-age analysis is a catch-length analysis which combines information on fishing effort, catch at length, growth, and natural mortality to estimate recruitment and population abundance. During the past decade, much progress has been made to improve catch-length analysis. Lai and Gallucci (1988) examined the effects of parameter variation on length-cohort analysis, Fournier and Doonan (1987) developed a length-based production model, and Schnute (1987) derived a general size-structured population model. Sullivan et al. (1990) constructed a catch-length analysis which incorporates stochastic growth and separates recruitment into year and

length components. However, most catch-length analyses were developed or applied to fish populations. Some size-frequency analyses have been conducted for decapods (Jones, 1979; Caddy, 1987; Fogarty and Idoine, 1988), but to our knowledge, few catch-length analyses have been applied to crabs.

Some commercially important crab populations are assessed annually by trawl surveys, and population abundances can be directly estimated from assessment data. Previously, we developed a length-based population model using such crab survey data to estimate population parameters and to improve abundance estimates (Zheng et al., 1995). However, for many crab populations the only usable data available are fishing effort and catch at length. Thus, a logical choice is to estimate abundance of crab populations using these data.

Our purpose in this study is to develop a catch-length analysis to estimate population size for unsurveyed crab populations. We modified the length-based population model developed by Zheng et al. (1995) for application to fishing effort and catch-at-length data that are routinely collected from many

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crab pot fisheries. The model incorporates stochastic growth, in which individual crabs molt with an annual molting probability and gradual recruitment over length. We applied our catch-length analysis to RKC populations in Bristol Bay and off Kodiak Island, Alaska. Bristol Bay RKC have supported one of the most valuable fisheries in the United States. The Kodiak RKC fishery was also very valuable before it collapsed in the early 1980's, and the population has failed to recover since then. We selected these stocks because both populations have been intensively studied during the last three decades and because data are available to estimate biological parameters such as growth and mortality. Moreover, the availability of annual trawl or pot survey data allowed us to compare population abundances estimated from the catch-length analysis and from surveys to determine the reliability of the catch-length analytical methods that we developed.

## Methods

### Data requirement

Data required for the model include annual length-frequency of commercial catches by shell condition, total annual catch and effort, the mean and variance in growth increment per molt, and natural mortality. Catch-length frequency and total fishing effort are available for most crab populations in Alaska. In this study we defined fishing effort as total annual pot lifts, i.e., the product of the total number of pots fished and the number of times each pot was deployed and retrieved in the fishery. The mean and variation in growth increment per molt can be estimated from tagging data, which are available for some crab populations.

In our study, we estimated the mean and variation in growth increments per molt for Bristol Bay and Kodiak RKC from studies by Balsiger (1974), Powell (1967), and Weber and Miyahara (1962). The model was fitted to RKC fishery data for Bristol Bay from 1974 to 1993 and for Kodiak from 1964 to 1982. Owing to low abundance, the Bristol Bay fishery was closed in 1994, and the Kodiak fishery has been closed since 1983. The RKC fisheries in Alaska harvest only male crabs, and the minimum legal carapace length (CL) is 135 mm for Bristol Bay RKC and 147 mm for Kodiak. Accordingly, we modeled only legal male crabs. The length frequency of catches was summarized by 5-mm intervals, and the largest length group included crabs  $\geq 165$  mm CL for Bristol Bay and  $\geq 182$  mm CL for Kodiak.

For comparisons, area-swept estimates of Bristol Bay legal male abundance were obtained from trawl

surveys conducted by the National Marine Fisheries Service (NMFS) (Stevens et al.<sup>1</sup>). Standardized catch per unit of effort (CPUE) from pot surveys and from tag and recovery data for Kodiak legal male crabs was provided by Peterson et al. (1986). We estimated mean catchability of the Kodiak pot survey using the Petersen mark-recapture equation and annual commercial catch, tag, and recovery data from 1973 to 1979. This allowed us to estimate annual legal male abundances by dividing relative abundance (standardized survey CPUE) by the catchability. These abundance estimates derived from survey data were not used in catch-length analyses but were instead compared to final results of catch-length analyses.

### Population model

The population model is similar to the length-based model for Bristol Bay RKC developed by Zheng et al. (1995). Mean growth increment per molt for length class  $i$ ,  $G_i$ , is assumed to be a linear function of mean carapace length  $l$  of the length class just before molting:

$$G_i = a + bl, \quad (1)$$

where  $a$  and  $b$  are the intercept and slope. Parameters  $a$  and  $b$  were estimated from Weber and Miyahara (1962) to be 13.140 and 0.018 for Bristol Bay, whereas we estimated them from Powell's (1967) data as 41.047 and  $-0.159$  for waters off Kodiak Island.

For flexibility, we chose a gamma distribution to describe the variation in growth increment per molt:

$$g(x | \alpha_i, \beta) = x^{\alpha_i - 1} e^{-x/\beta} / (\beta^{\alpha_i} \Gamma(\alpha_i)), \quad (2)$$

where  $x$  is growth increment per molt,  $\alpha_i$  and  $\beta$  are parameters, and  $\alpha_i = G_i / \beta$ . The expected proportion of crabs molting from length class  $i'$  to length class  $i$  is equal to the integral of the gamma function over the length interval  $[i_1, i_2]$  of the receiving length class  $i$ :

$$P_{i', i} = \int_{i_1}^{i_2} g(x | \alpha_i, \beta) dx, \quad (3)$$

where  $l$  is the mean length of length class  $i'$ . For the last length class  $L$ ,  $P_{L, L} = 1$ . The variation in growth increment per molt,  $\beta$ , for both populations was set to 0.75, which produced a transitional matrix similar to that estimated by Balsiger (1974) for Bristol Bay RKC.

<sup>1</sup> Stevens, B. G., R. A. MacIntosh, J. A. Haaga, and J. H. Bowerman. 1993. Report to industry on the 1993 eastern Bering Sea crab survey. Alaska Fish. Sci. Center., Natl. Mar. Fish. Serv., NOAA, Seattle, WA, Proc. Rep. 93-14, 53 p.

The molting probability for a given length class and time  $t$  is modeled by a logistic function:

$$m_{i,t} = 1 - \frac{1}{1 + \phi_i e^{-\omega_i t}}, \quad (4)$$

where  $\phi_i$  and  $\omega_i$  are parameters, and  $t$  is the mean length of length class  $i$ . Different logistic functions were used to describe the molting probabilities during different periods. The molting probabilities during different years were grouped to produce a good fit. Three groups were selected for the Bristol Bay RKC: group 1 includes 1974–76, 1980, 1987–88, and 1992–93; group 2 covers 1981–86; and group 3 includes 1977–79 and 1989–91. Two groups were made for the Kodiak RKC: group 1 includes 1964–65, 1972, and 1980–82 and group 2 includes 1966–71 and 1973–79.

Recruitment into the exploitable population is separated into two components: 1) total recruits for year  $t$  entering the exploitable population,  $R_t$ , and 2) the proportion of recruits belonging to each length class,  $U_i$ . This is expressed by

$$R_{i,t} = R_t U_i, \quad (5)$$

where  $U_i$  is described by a gamma distribution for flexibility, such as in Equations 2 and 3, with parameters  $\alpha_r$  and  $\beta_r$ .

To reduce the number of parameters, we assumed that new-shell and old-shell crabs have the same natural mortality and probability of molting the following year (Zheng et al., 1995). The annual abundance of new-shell crabs is the combined result of growth, mortality, and recruitment:

$$N_{i+1,t+1} = \sum_{i'=1}^{i+1} P_{i',i+1} \left[ \sum_p \left[ (CN_{i',t,p} + CO_{i',t,p}) e^{(T_{i,p}-1)M} \right] m_{i',t} \right] \times + R_{i+1,t+1}, \quad (6)$$

where  $N_{i,t}$  and  $O_{i,t}$  are the respective abundances of new-shell and old-shell crabs in length class  $i$  on 1 July in year  $t$ ;  $CN_{i,t,p}$  and  $CO_{i,t,p}$  are the commercial catches of new-shell and old-shell crabs in length class  $i$ , year  $t$ , and fishing period  $p$ ;  $M$  is instantaneous natural mortality; and  $T_{i,p}$  is the period from 1 July to the mid-point of fishing period  $p$  in year  $t$ . All recruits are new-shell crabs. Old-shell crabs are crabs that did not molt the previous year:

$$O_{i+1,t+1} = \left( \frac{(N_{i+1,t} + O_{i+1,t}) e^{-M} - \sum_p \left[ (CN_{i+1,t,p} + CO_{i+1,t,p}) e^{(T_{i,p}-1)M} \right]}{1 - m_{i+1,t}} \right) (1 - m_{i+1,t}). \quad (7)$$

The new-shell and old-shell crabs in the last length class were lumped together.

There was only one fishing period each year for the Bristol Bay RKC fishery and for the Kodiak RKC fishery prior to 1974. A second fishing period that targeted large crabs occurred for the Kodiak fishery each year from 1974 to 1982. The catch in the second fishing period was about 10% of that in the first period. We did not use the fishing efforts in the second period because the efforts targeted only a small proportion of the population and were relatively small.

For the first fishing period, the catch by length was estimated as

$$\begin{aligned} CN_{i,t,1} &= TC_{t,1} s_{i,1} N_{i,t} / TB_{t,1}, \\ CO_{i,t,1} &= TC_{t,1} s_{i,1} O_{i,t} / TB_{t,1}, \end{aligned} \quad (8)$$

where  $TC_{t,1}$  is total annual observed catch for the first fishing period, and  $TB_{t,1}$  is estimated exploitable abundance on 1 July in year  $t$ , i.e.

$$TB_{t,1} = \sum_i [s_{i,1} (N_{i,t} + O_{i,t})], \quad (9)$$

and  $s_{i,1}$  is the selectivity coefficient in length class  $i$  for the first fishing period. Parameters  $s_{1,1}$  and  $s_{2,1}$  were estimated for each population, and selectivity coefficients for length class 3 or larger were set to one.

The annual fishing effort for the first fishing period was

$$f_t = TC_{t,1} / (q MB_{t,1}), \quad (10)$$

where  $q$  is catchability coefficient for the fishery and  $MB_{t,1}$  is mean exploitable abundance during the first fishing period in year  $t$  and approximated as

$$MB_{t,1} = TB_{t,1} e^{-T_{i,1} M} - 0.5 TC_{t,1}. \quad (11)$$

During the second fishing period for the Kodiak RKC fishery, there were minimum size limits of 168 mm CL from 1974 to 1977, and 157.5 mm CL from 1978 to 1982. Two parameter values,  $\theta_{s1}$  and  $\theta_{s2}$ , were estimated for the two minimum size limits:

$$s_{i,t,2} = (e^{(t-i)^2 \theta_{s1}} - 1) / s_{L,t,2}, \quad (12)$$

where  $\bar{l}$  is the mean length of length class  $i$ , and  $\bar{l}'$  and  $L$  are the mean lengths of the first and last length classes. This selectivity function was chosen, based on the differences of the catch-length frequencies between the first and second fishing periods.

The catch by length for the second fishing period was estimated as

$$\begin{aligned} CN_{i,t,2} &= TC_{i,2} s_{i,t,2} (N_{i,t} e^{-T_{i,1}M} - CN_{i,t,1}) / TB_{i,2}, \\ CO_{i,t,2} &= TC_{i,2} s_{i,t,2} (O_{i,t} e^{-T_{i,1}M} - CO_{i,t,1}) / TB_{i,2}, \end{aligned} \quad (13)$$

where  $TC_{i,2}$  is total annual observed catch for the second fishing period and  $TB_{i,2}$  is estimated exploitable abundance just after the first fishing period in year  $t$ , i.e.

$$TB_{i,2} = \sum_i \left[ s_{i,t,2} \begin{pmatrix} (N_{i,t} + O_{i,t}) e^{-T_{i,1}M} \\ - CN_{i,t,1} - CO_{i,t,1} \end{pmatrix} \right]. \quad (14)$$

**Parameter estimation**

Model parameters were estimated under the assumption of log normally distributed measurement or observation errors for length compositions of catches and annual fishing efforts. In Alaska, catch data are legally required for sales transactions between fishermen and processors, and it is generally believed that total annual crab catches in Alaska are fairly accurately reported. Thus, no measurement error was imposed on total annual catch for the catch-length analysis. A nonlinear least squares approach was used to minimize the residual sum of squares (RSS) of length compositions of catches and annual effort:

$$\begin{aligned} RSS &= \sum_{i,t,p} \left[ \left( \ln(CN_{i,t,p} + c) - \ln(\tilde{C}N_{i,t,p} + c) \right)^2 + \right. \\ &\quad \left. \left( \ln(CO_{i,t,p} + c) - \ln(\tilde{C}O_{i,t,p} + c) \right)^2 \right] \\ &\quad + \lambda^2 \sum_i \left[ \left( \ln(f_t + 1) - \ln(\tilde{f}_t + 1) \right)^2 \right], \end{aligned} \quad (15)$$

where  $\tilde{C}N_{i,t,p}$  and  $\tilde{C}O_{i,t,p}$  are observed catches for new-shell and old-shell crabs in length class  $i$ , year  $t$ , and fishing period  $p$ ;  $f_t$  is observed fishing effort in year  $t$  for the first fishing period each year;  $\lambda$  is an error weighting factor for fishing effort relative to catch composition; and  $c$  is a constant set equal to  $0.01 \times 10^6$

crabs to avoid taking the logarithm of zero and to reduce the impact of extremely small catches on parameter estimation. Generally,  $c$  should be relatively small compared to total catch, but estimation may fail to converge for a very small  $c$ .

The subroutine DBCLSF of IMSL FORTRAN (IMSL, 1991) was used to perform nonlinear least-squares parameter estimation through a modified Levenberg-Marquardt algorithm and a finite-difference Jacobian. All parameters were bounded to be nonnegative.

The following model parameters were estimated for each population: recruits for each year, except the first year; total abundance in the first year; parameters  $\alpha_r$  and  $\beta_r$ ; molting probability parameters  $\phi_l$  and  $\omega_p$ ; selectivity parameters  $s_{1,1}$ ,  $s_{2,1}$ ,  $\theta_{s1}$  and  $\theta_{s2}$ ; and catchability coefficient  $q$ . Starting in the second year, the abundances by length, sex, and shell condition were computed recursively from 1) the abundances by length and shell condition in the first year, 2) annual recruitment, 3) catch, and 4) model parameters. To reduce parameters further, we used the observed frequencies of length and shell classes from first-year catch data to approximate the true catch frequencies. Thus, we had to estimate only total abundance of male crabs for the first year.

Initial values of parameters were approximated by using catch data. A 40% harvest rate was used to convert total catch in the first year into total abundance and the sum of the new-shell catch in the first four length classes each year into recruitment (Zheng et al., 1995). Initial values were interactively updated; the estimated parameters for the first run were used as the initial parameters for the second run, and so on, until no further reduction of total RSS could be made.

Because we did not know the ratio between the variance of catch by length and the variance of fishing effort, we could not use a maximum likelihood approach. Instead, we used seven error weighting factors ( $\lambda$ ): 0, 1, 2, 3, 5, 7, and 10 to conduct alternative catch-length analyses and compared the results for different weighting factors.

We did not estimate natural mortality but used several natural mortalities for comparisons. Kruse and Collie<sup>2</sup> and Collie<sup>3</sup> used 0.3 as instantaneous natural mortality for the Bristol Bay and Kodiak le-

<sup>2</sup> Kruse, G. H., and J. S. Collie. 1991. Preliminary application of a population size estimation model to the Bristol Bay stock of red king crabs. Alaska Dep. Fish Game, Comm. Fish. Div., Reg. Information Rep. 5J91-09, 25 p.

<sup>3</sup> Collie, J. S. 1991. Estimating the abundance of king crab populations from commercial catch and research survey data. Rep. to Alaska Dep. Fish Game. Univ. Alaska, Fairbanks, Rep. 91-03, 27 p.

gal male RKC. Besides 0.3, we also used  $M$  of 0.2, 0.4, and 0.5 in our analyses for both populations. In addition, variable natural mortalities—0.2 for periods of 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82—were used for the Bristol Bay population for comparisons based on our previous work with this stock (Zheng et al., 1995).

## Results

### Bristol Bay red king crab

Model parameter estimates for Bristol Bay RKC depend on natural mortality and weighting factor

(Table 1). Higher natural mortality generally resulted in a higher total abundance in the first year and higher annual recruitment. Higher weights applied to fishing effort produced larger total  $RSS$ , whereas an intermediate weight resulted in the highest  $RSS$  contributed by the fishing effort (Table 1). For a weighting factor of one, total  $RSS$  were similar and ranged from 23.4 to 24.8 for all fits (Table 1). Catchability coefficient was negatively associated with natural mortality. Selectivity coefficients were less than one for the first length class for all fits and equal to about one for all other length classes.

The abundances of Bristol Bay legal male RKC estimated from the trawl surveys conducted by NMFS changed dramatically during the last two

**Table 1**

Summary of parameter estimates by the catch-length analysis for the Bristol Bay red king crab, *Paralithodes camtschaticus*, population for eight fits. Recruits are in thousands of crabs. Variable  $M$  is 0.2 for 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82. Total  $RSS$  ( $RSS_{tot}$ ) is equal to the  $RSS$  of length compositions of catches ( $RSS_c$ ) and annual effort ( $RSS_e$ ).

	$M=0.3$ $\lambda=0$	$M=0.3$ $\lambda=1$	$M=0.3$ $\lambda=3$	$M=0.3$ $\lambda=10$	$M=0.2$ $\lambda=1$	$M=0.4$ $\lambda=1$	$M=0.5$ $\lambda=1$	$M=var$ $\lambda=1$
$\alpha_r$	232.743	244.608	194.611	188.020	222.013	208.456	182.513	223.248
$\beta_r$	0.6127	0.5824	0.7249	0.7546	0.6407	0.6761	0.7664	0.6355
$\phi_1$	138,820	76,821	105,956	20,075	99,974	257,671	388,794	182,935
$\omega_1$	0.0805	0.0750	0.0763	0.0658	0.0770	0.0832	0.0864	0.0812
$\phi_2$	5,193.0	5,136.2	5,157.8	2,699.4	5,424.3	2,818.5	1,797.6	4,666.4
$\omega_2$	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000
$\phi_3$	385,353	4,634,955	3,093,737	579,222	1,537,110	10,721,570	5,192,095	2,621,660
$\omega_3$	0.0773	0.0944	0.0935	0.0836	0.0876	0.1001	0.0954	0.0906
$q$	NA	0.0023	0.0022	0.0024	0.0028	0.0019	0.0016	0.0024
$S_{1,1}$	0.9834	0.9008	0.8289	0.9379	0.9520	0.7820	0.7412	0.8329
$S_{2,1}$	0.9974	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
$N_{74}$	19,732.5	21,360.0	20,537.7	18,295.4	17,630.4	25,811.1	31,131.7	18,345.1
$R_{75}$	15,852.5	16,650.6	16,700.4	16,446.1	14,052.6	19,849.8	23,623.7	14,647.9
$R_{76}$	14,501.8	14,250.6	13,648.1	13,131.0	12,358.8	16,829.6	19,824.2	12,922.0
$R_{77}$	24,927.0	22,896.5	17,450.5	13,745.3	18,518.2	27,286.2	32,225.9	21,283.3
$R_{78}$	34,971.4	34,473.4	27,690.5	22,081.5	26,614.2	40,847.3	47,167.4	33,598.9
$R_{79}$	24,073.3	25,932.3	27,849.9	28,343.4	23,378.7	29,761.8	33,153.0	27,839.3
$R_{80}$	18,409.0	19,090.3	22,253.7	21,837.6	19,488.9	20,820.4	22,445.6	25,626.7
$R_{81}$	1,958.6	2,096.8	2,299.2	3,230.2	1,995.5	2,243.9	2,437.9	3,178.3
$R_{82}$	354.1	997.2	1,452.6	1,111.6	787.7	1,404.6	1,986.8	1,502.9
$R_{83}$	547.6	149.8	286.6	229.0	135.9	157.0	174.2	774.0
$R_{84}$	1,084.5	1,333.0	2,111.7	2,411.7	1,094.2	1,694.5	2,240.7	1,559.8
$R_{85}$	1,343.6	1,602.3	2,208.4	2,350.4	1,292.2	2,059.8	2,749.6	1,345.3
$R_{86}$	2,582.5	2,830.2	3,071.4	3,297.8	2,318.2	3,559.0	4,622.2	2,405.0
$R_{87}$	4,437.1	5,201.8	4,268.0	2,782.2	3,815.0	6,867.2	9,075.5	4,066.3
$R_{88}$	5,317.7	5,223.7	3,535.5	2,759.2	3,793.1	6,895.0	9,125.6	4,131.9
$R_{89}$	7,244.1	6,304.6	4,104.7	3,043.8	4,785.9	8,000.4	10,285.6	5,269.1
$R_{90}$	4,616.4	4,792.3	5,413.8	5,681.4	4,034.9	5,866.9	7,268.1	4,194.0
$R_{91}$	4,134.6	4,396.6	5,020.9	4,858.1	3,704.9	5,424.8	6,758.2	3,894.6
$R_{92}$	1,420.0	1,527.6	1,713.1	1,357.2	1,293.8	1,879.8	2,322.0	1,382.3
$R_{93}$	3,489.0	3,489.4	4,126.9	4,234.4	2,953.3	4,182.8	5,090.3	3,393.6
$RSS_{tot}$	19.957	24.659	35.028	45.685	24.844	23.999	23.782	23.356
$RSS_c$	19.957	20.999	30.030	42.629	21.437	20.595	20.461	19.839
$RSS_e$	0.000	3.660	4.998	3.066	3.407	3.404	3.321	3.517

decades (Stevens et al.<sup>1</sup>). The abundances peaked in the late 1970's and then declined more than 30-fold during the early 1980's (Fig. 1). A moderate recovery occurred in the late 1980's and early 1990's; then abundances decreased again during the last three years. The estimated abundances by different weighting factors with natural mortality of 0.3 generally reflected this trend of crab abundance with different accuracies, although modeled estimates were generally lower than the survey abundances (Fig. 1). The commercial CPUE was adjusted to the same scale as abundances to facilitate comparison, but it did not track well with the abundance trend estimated from the trawl surveys. The CPUE's were much higher in 1974 and 1975 and much lower in 1977 and 1978 than expected from the survey data. The CPUE's from 1984 to 1993 fluctuated around a low level, whereas the abundance increased and then decreased during the same period (Fig. 1). The estimated abundances from catch-length analyses with  $\lambda = 0$  and  $\lambda = 1$  were very similar, but the abundances in recent years tended to increase beyond a reasonable level without constraints on fishing effort or the recruitment in the terminal year for  $\lambda = 0$ . The upper limit of recruitment in the terminal year (1993) with  $\lambda = 0$  was set to that estimated with  $\lambda = 1$  to stabilize estimates. High weighting factor,  $\lambda = 3$  or  $\lambda = 10$ , forced the abundance estimates close to the trend of CPUE. Overall the estimated abundance with  $\lambda = 1$  most closely followed the trend of survey abundances (Fig. 1).

The estimated abundances with different instantaneous natural mortality rates followed the trend of survey abundances, and higher natural mortali-

ties resulted in higher abundance estimates (Fig. 2). Generally,  $M = 0.4$  produced absolute abundance estimates closer to the trawl survey than other natural mortalities. Variable natural mortality, expressed as three different levels, produced abundance estimates between those with  $M$  of 0.2 and 0.5, providing improvement in abundance estimates only during the early 1980's when high natural mortality occurred (Fig. 2).

The observed catches by length were compared to estimated catches by length from the model fit with  $\lambda = 1$ , with constant  $M$  of 0.3 and 0.5, and with three levels of  $M$  (Fig. 3). All three fits of the model produced similar catches by length and fit the observed data very well.

The observed and estimated fishing efforts have a similar overall trend but differed by up to 50% in some years (Fig. 4). As expected, larger weighting factors resulted in estimates of fishing effort closer to the observed level.

To explore further the effects of parameters  $\lambda$  and  $M$  on model results, we compared estimated length compositions of recruits and molting probabilities for the two most disparate fits (Fig. 5). There was very little variation in length compositions of recruits among different fits. The difference in molting probabilities was less than 15% between any two fits for any given length class within the same time period (Fig. 5) and was less than 5% among most fits for a given length class. The average molting probabilities from all fits for the first group of years were similar to the average molting probabilities estimated by Zheng et al. (1995) from the survey data with one exception. The molting probabilities for the period 1980-

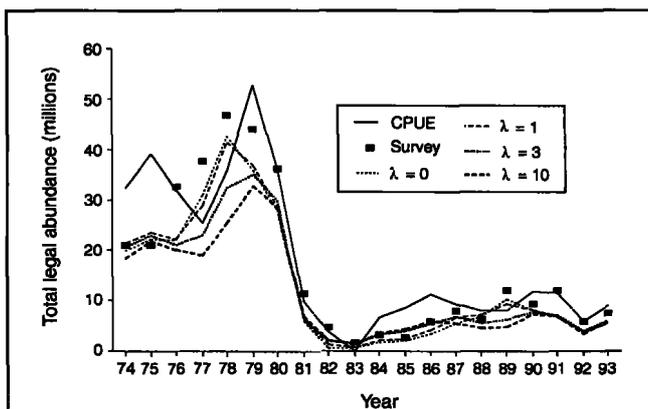


Figure 1

Comparison of estimates of total legal male abundance for Bristol Bay red king crab, with  $M = 0.3$  and with different weighting factors ( $\lambda$ ). The fishery CPUE (mean catch of legal male crabs per pot lift) was scaled to the same level as abundances. Also shown are NMFS trawl survey estimates of abundance.

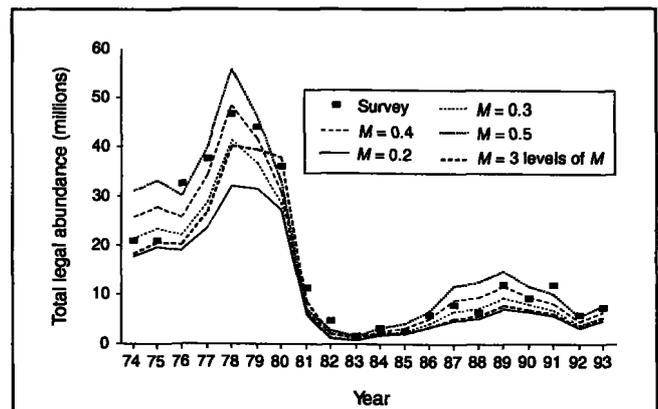
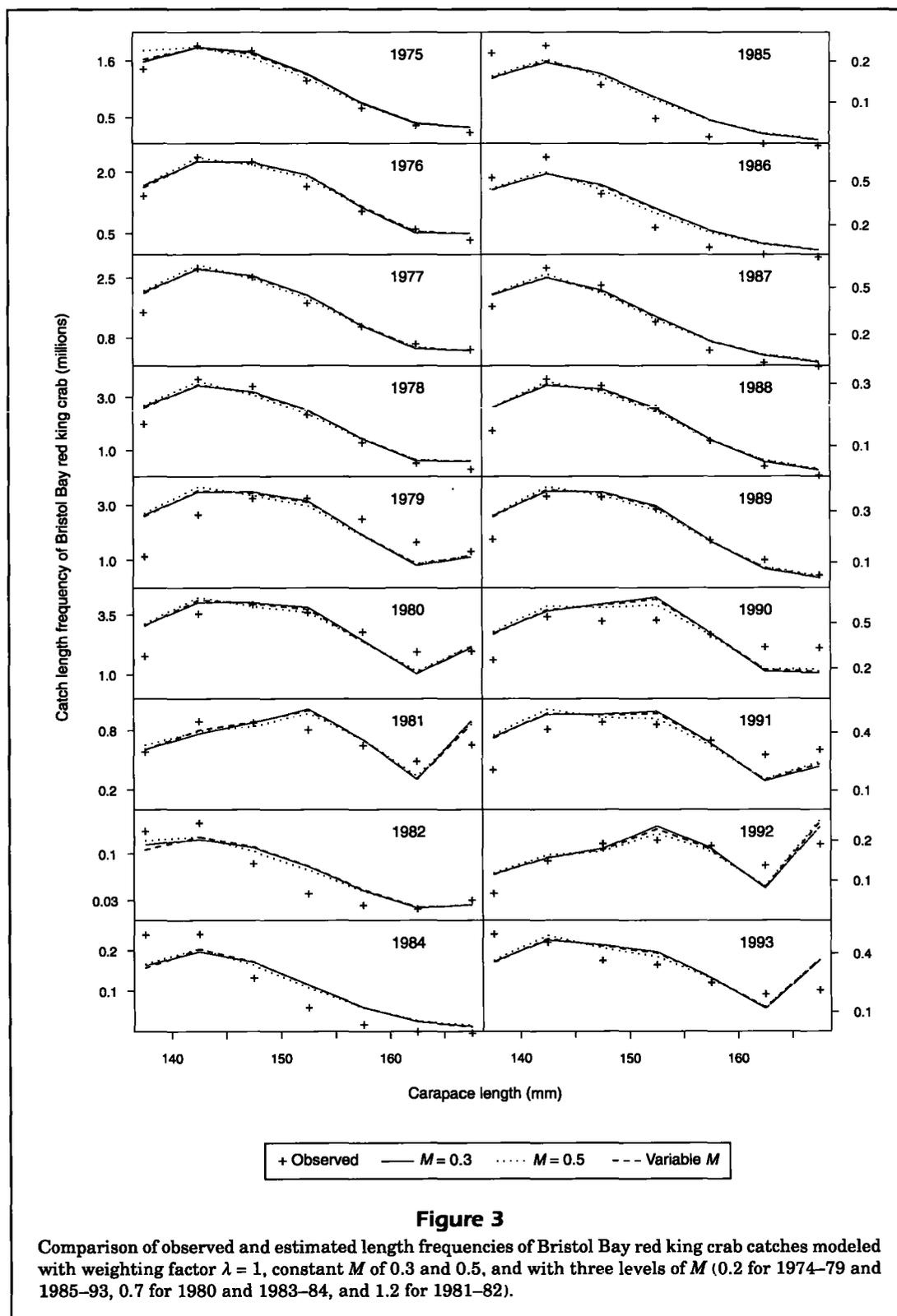


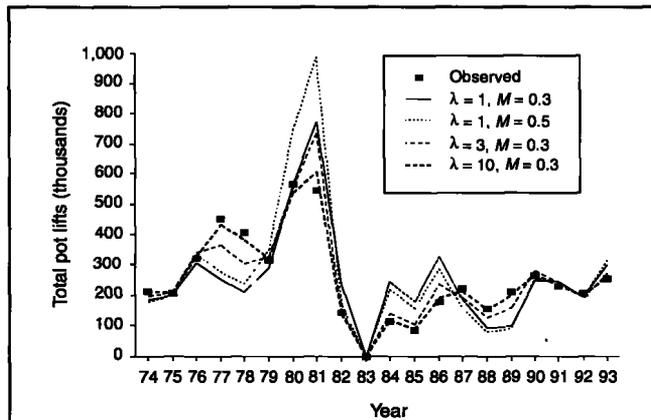
Figure 2

Comparison of estimates of total legal male abundance for Bristol Bay red king crab modeled with weighting factor  $\lambda = 1$  and with either constant or variable  $M$  at three levels: 0.2 for 1974-79 and 1985-93, 0.7 for 1980 and 1983-84, and 1.2 for 1981-82. Trawl survey estimates of abundance are also shown for comparison.



86 were estimated to be zero, which is biologically unrealistic. The zero molting probabilities were primarily caused by few large new-shell crabs in the catch

during this period. The average molting probabilities from all fits during 1977–79 and 1989–91 were slightly higher than those estimated by Zheng et al. (1995).



**Figure 4**

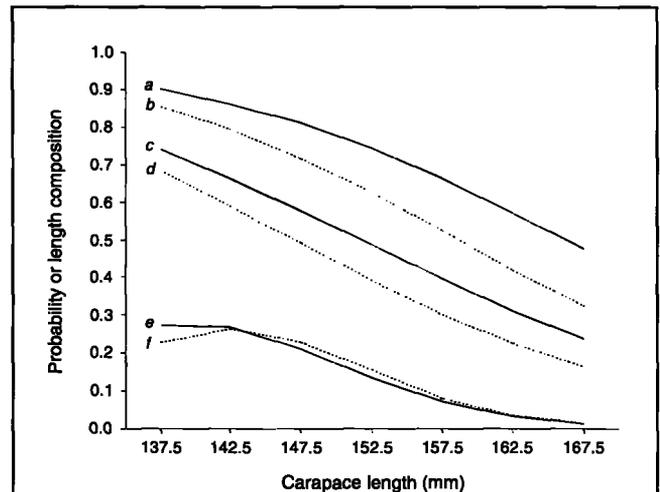
Comparison of observed and estimated fishing efforts of the Bristol Bay red king crab fishery modeled with weighting factor  $\lambda = 1$  and constant  $M$  of 0.3 and 0.5 and with weighting factor  $\lambda = 3$  and 10 and constant  $M$  of 0.3.

**Kodiak Island red king crab**

As in the case of Bristol Bay RKC, the abundance in the first year and annual recruitment of red king crab off Kodiak Island were mainly affected by natural mortality and the weighting factor (Table 2). For all fits, the recruitment in 1965 was much higher than those in other years. With  $\lambda = 1$ , total RSS decreased slightly with increasing natural mortality, whereas the RSS contributed by fishing effort increased (Table 2). Higher weighting factors resulted in higher total RSS (Table 2). For the first fishing period, selectivity coefficients for the first length class were about 0.5, and no selectivity was detected for the other length classes (Table 2). For the second fishing period, catches concentrated on large-size crabs.

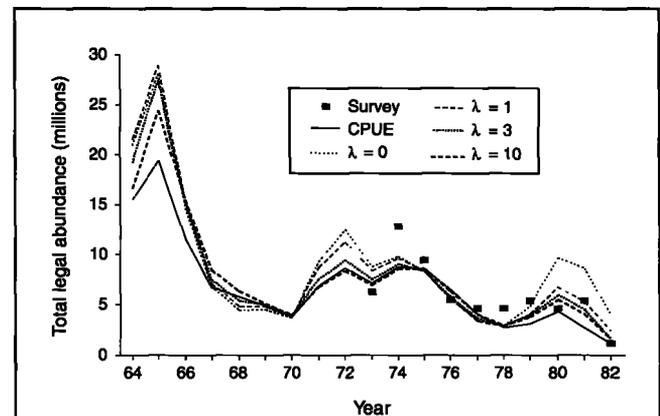
The estimated legal male abundances of Kodiak RKC peaked in 1965 and fell to a very low level in the late 1960's (Fig. 6). The population moderately recovered in the early and middle 1970's but declined again in the late 1970's and completely collapsed after 1982. Model estimates of abundance with  $M = 0.3$  and different weighting factors basically followed the same trends as the fishery CPUE and the abundances estimated by pot surveys (Fig. 6). Note that no survey data were available until 1973 (Peterson et al., 1986). Like the results for Bristol Bay RKC, the abundance estimates with  $\lambda = 1$  followed the trend of survey abundances best among all fits. The scaled CPUE was very close to survey abundance estimates from 1973 to 1977 but were much lower from 1978 to 1981.

Similar to Bristol Bay RKC, the estimated abundances for Kodiak RKC with different natural mor-



**Figure 5**

Comparisons of length compositions of recruits (e:  $\lambda=0$  and  $M=0.3$ , f:  $\lambda=10$  and  $M=0.3$ ), molting probabilities during periods 1974–76, 1980, 1987–88, and 1992–93 (c:  $\lambda=5$  and  $M=0.3$ , d:  $\lambda=1$  and  $M=0.3$ ), and during periods 1977–79 and 1989–91 (a:  $\lambda=1$  and  $M=0.5$ , b:  $\lambda=0$  and  $M=0.3$ ) from the two most disparate fits among all model fits for Bristol Bay red king crab.



**Figure 6**

Comparison of estimates of total legal male abundance for Kodiak red king crab with  $M$  of 0.3 and different weighting factors ( $\lambda$ ). The fishery CPUE was scaled to the same level as abundances.

talities had a similar trend over time, and a higher natural mortality produced higher abundance estimates (Fig. 7). The estimated abundances with natural mortality of 0.2 were lower than survey abundances for most years, whereas the abundances estimated with natural mortality of 0.5 were generally higher. With  $M = 0.4$ , the closest abundance estimates to survey abundances were produced among all fits (Fig. 7).

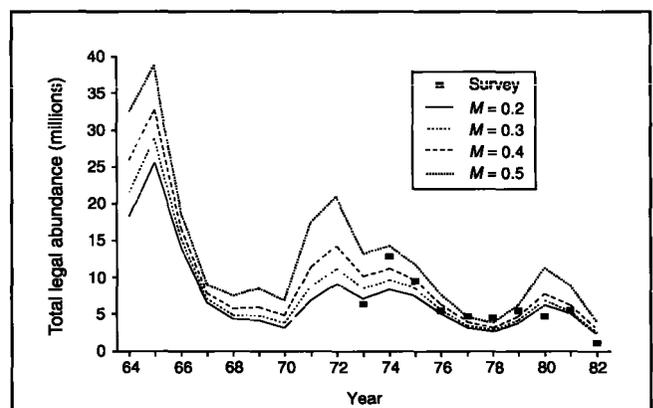
**Table 2**

Summary of parameter estimates by the catch-length analysis for the Kodiak red king crab population for seven fits. Recruits are in thousands of crabs. Total  $RSS (RSS_{tot})$  is equal to the  $RSS$  of length compositions of catches ( $RSS_c$ ) and annual effort ( $RSS_e$ ).

	$M=0.3$ $\lambda=0$	$M=0.3$ $\lambda=1$	$M=0.3$ $\lambda=3$	$M=0.3$ $\lambda=10$	$M=0.2$ $\lambda=1$	$M=0.4$ $\lambda=1$	$M=0.5$ $\lambda=1$
$\alpha_r$	81.727	35.562	39.570	34.371	39.576	33.364	37.299
$\beta_r$	1.7562	3.4703	3.2294	3.6075	3.2052	3.6289	3.2795
$\phi_1$	147.272	135,590	134,336	246,181	121,736	142,585	656,736
$\omega_1$	0.0674	0.0679	0.0684	0.0732	0.0671	0.0683	0.0769
$\phi_2$	258,686	5,900,997	5,859,429	6,001,626	5,215,578	5,681,410	3,532,557
$\omega_2$	0.0787	0.0982	0.0981	0.0981	0.0972	0.0982	0.0952
$q$	NA	0.0045	0.0047	0.0048	0.0050	0.0038	0.0029
$S_{1,1}$	0.5520	0.4481	0.4649	0.4560	0.4538	0.4466	0.4460
$S_{2,1}$	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
$\theta_{e1}$	1.0e-6	1.0e-6	1.0e-6	0.0003	1.0e-6	0.0002	0.0004
$\theta_{e2}$	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6
$N_{64}$	20,944.8	21,537.4	19,273.2	16,664.7	18,173.0	25,863.5	32,485.1
$R_{65}$	17,684.0	18,482.6	18,412.5	17,298.9	16,460.5	20,938.2	24,625.0
$R_{66}$	4,592.4	5,330.7	6,662.2	8,951.2	4,873.5	5,831.0	6,222.7
$R_{67}$	2,796.0	3,078.2	3,647.5	5,127.5	2,798.5	3,417.3	3,878.6
$R_{68}$	3,316.6	3,619.0	4,046.4	4,529.1	3,164.2	4,274.9	5,632.4
$R_{69}$	3,461.8	3,621.5	3,525.1	3,125.5	3,045.6	4,492.4	6,385.9
$R_{70}$	2,121.7	2,158.9	2,043.8	2,029.3	1,795.0	2,707.4	3,880.0
$R_{71}$	8,046.7	7,480.9	6,209.6	5,328.2	5,918.3	9,819.2	15,043.5
$R_{72}$	8,586.0	7,634.8	6,320.9	5,610.1	6,186.2	9,740.1	14,467.9
$R_{73}$	4,095.6	4,263.0	4,037.3	3,766.8	3,574.5	5,190.1	6,710.2
$R_{74}$	5,185.5	5,405.2	5,448.1	5,466.6	4,647.3	6,423.0	8,182.8
$R_{75}$	4,116.1	4,407.9	4,809.2	5,360.7	3,835.2	5,143.3	6,362.9
$R_{76}$	2,266.6	2,464.4	2,753.0	3,264.4	2,152.7	2,859.6	3,463.3
$R_{77}$	1,416.1	1,495.0	1,599.8	1,835.6	1,323.9	1,702.9	2,033.7
$R_{78}$	1,837.0	1,816.9	1,723.0	1,573.6	1,645.5	2,034.8	2,493.3
$R_{79}$	4,074.1	3,510.5	3,232.3	3,008.8	3,210.3	3,956.7	5,256.6
$R_{80}$	8,327.1	5,879.3	5,147.0	4,672.7	5,410.7	6,762.5	9,835.9
$R_{81}$	6,295.2	4,101.1	3,556.5	3,271.2	3,825.8	4,814.7	6,714.1
$R_{82}$	1,889.0	1,888.9	1,400.1	1,474.6	1,773.6	2,230.5	2,315.5
$RSS_{tot}$	35.584	41.165	46.751	53.170	42.361	39.801	36.519
$RSS_c$	35.584	39.828	43.379	51.876	40.908	38.176	34.181
$RSS_e$	0.000	1.337	3.372	1.294	1.453	1.625	2.338

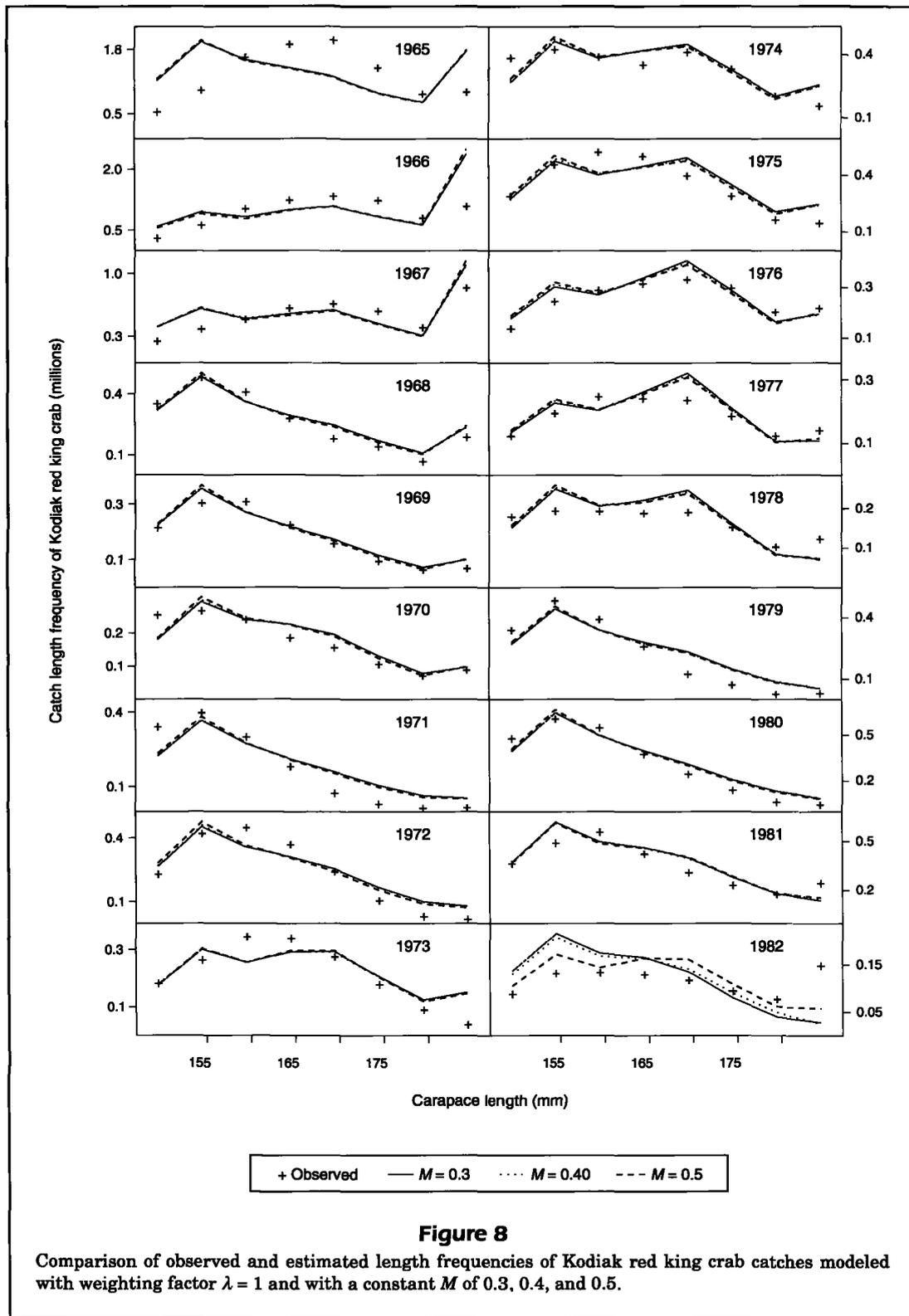
The observed catches by length were compared to estimated catches by length from the model fit with  $\lambda = 1$  and with constant  $M$  of 0.3, 0.4, and 0.5 (Fig. 8). All three fits of the model produced similar catches by length and fitted the observed data very well, except data for 1965 and 1982. The poor fit in 1965 was mainly caused by the observed catch-length composition in the initial year (1964). The rapid expansion of fishing grounds during this period made the catch-length compositions inconsistent between these two years. The catch in 1982 was extremely low in comparison to the past annual catches.

The fishing effort was very high during the mid-1960's and the early 1980's (Fig. 9). Like Bristol Bay RKC, larger weighting factors produced estimates of fishing effort closer to the observed effort. With  $\lambda = 1$ , a constant  $M$  of 0.3 fitted the fishing effort much better than a constant  $M$  of 0.5 (Fig. 9).



**Figure 7**

Comparison of estimates of total legal male abundance for Kodiak red king crab modeled with weighting factor  $\lambda = 1$  and different values of  $M$ .

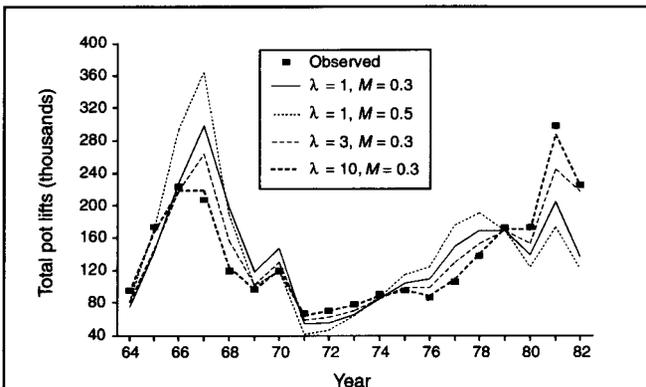


Similar to Bristol Bay RKC, there was very little difference in length compositions of recruits among all fits (Fig. 10). The difference in molting probabilities was generally less than 10% between any two

fits for any given length class (Fig. 10) and was less than 2% among most fits for a given length class. Molting probabilities for the first group of years were much higher than the second group.

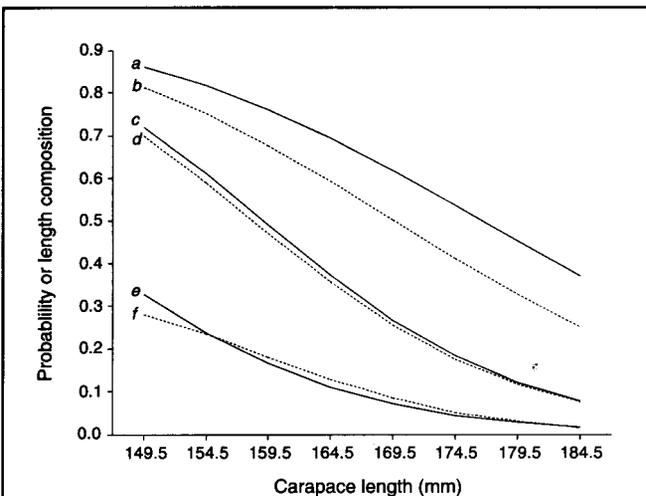
## Discussion

Two alternative models have been developed for RKC populations. A measurement error model using catch and survey data was developed to smooth out measurement errors in abundance estimates of legal male crabs composed of two groups: recruits and post-recruits (Collie and Kruse, in press; Kruse and Collie<sup>2</sup>; Collie<sup>3</sup>). The expanded version of the measurement error model is a length-based population model



**Figure 9**

Comparison of observed and estimated fishing efforts of the Kodiak red king crab fishery modeled with weighting factor  $\lambda = 1$  and constant  $M$  of 0.3 and 0.5 and with weighting factor  $\lambda = 3$  and 10 and constant  $M$  of 0.3.



**Figure 10**

Comparisons of length compositions of recruits (*e*:  $\lambda=0$  and  $M=0.3$ , *f*:  $\lambda=10$  and  $M=0.3$ ), molting probabilities during periods 1966–71 and 1973–79 (*c*:  $\lambda=1$  and  $M=0.2$ , *d*:  $\lambda=1$  and  $M=0.5$ ), and during periods 1964–65, 1972, and 1980–82 (*a*:  $\lambda=1$  and  $M=0.5$ , *b*:  $\lambda=0$  and  $M=0.3$ ) from the two most disparate fits among all model fits for Kodiak red king crab.

that incorporates stochastic growth and gradual recruitment over length and that estimates abundances of mature crabs of both sexes (Zheng et al., 1995). The length-based model also provides a means to study stock-recruitment relationships and can be used to evaluate harvest strategies. The catch-length analysis we developed in this study is a simplified version of the length-based model constructed by Zheng et al. (1995) and is meant to be applied to crab populations for which no surveys are conducted. The length-based model estimates abundance by producing the best fit to length-frequency data from the survey, and the catch-length analysis estimates abundance by producing the best fit to length-frequency and fishing-effort data from the commercial fleet. The catch-length analysis generally provides accurate estimates of trends of relative population abundances and gives reasonable estimates of absolute abundances provided that  $M$  can be approximated.

The legal male crab abundances estimated from the survey data for both populations were assumed to be absolute and were used to gauge the reliability of the catch-length analysis. A systematic approach was used to survey both populations with complete coverage of areas occupied by large-size crabs (Peterson et al., 1986; Stevens et al.<sup>4</sup>). The length frequency of crabs caught by the survey gears in Bristol Bay and Kodiak indicated that the selectivity of legal male crabs is about equal to one. Catchability of survey gears is difficult to estimate. Zheng et al. (1995) assumed the catchability of the trawl survey for Bristol Bay legal male RKC to be one, and Collie and Kruse (in press) showed that catchabilities of legal male RKC for both populations are close to one. Therefore, our assumption of absolute crab abundances from the survey estimates is reasonable. If this assumption is invalid, the survey abundances still represent relative population abundances, but we cannot use them to compare different levels of natural mortality in the catch-length analysis.

The most important parameter affecting total abundance estimates from the catch-length analysis is  $M$ , which has to be estimated separately from the analysis. Published natural mortalities for RKC vary greatly from one study to another and are probably a function of time and length (Schmidt and Pengilly, 1993; Zheng et al., 1995). A constant  $M$  of 0.3 was assumed for both Bristol Bay and Kodiak legal male RKC (Kruse and Collie<sup>2</sup>; Collie<sup>3</sup>; NPFMC<sup>4</sup>). Our re-

<sup>4</sup> NPFMC (North Pacific Fishery Management Council). 1990. Environmental assessment for Amendment 1 to the fishery management plan for the commercial king and Tanner crab fisheries in the Bering Sea/Aleutian Islands. North Pacific Fishery Management Council, Anchorage, AK, 27 p.

sults indicate that a constant  $M$  of 0.4 provides population abundance estimates closest to the abundances estimated by survey data for both RKC populations. Unlike the results from Zheng et al. (1995), variable  $M$  over time improved only slightly the abundance estimates from catch-length analysis. Because it is difficult to estimate  $M$  for crab populations, we suggest that a sensitivity study should be conducted to examine the effect of  $M$  on estimated abundances. Although  $M$  affects absolute abundance greatly, relative abundance is fairly robust to changes in  $M$ . Thus, if we are mainly interested in recruitment or population trends, such as those used in fishery oceanography, then uncertainty of  $M$  is not a big concern. On the other hand, if we wish to manage an unsurveyed crab stock with a fixed exploitation rate strategy,  $M$  must be known fairly accurately in order to avoid consistent over- or under-harvest.

In contrast to  $M$ , weighting factor  $\lambda$  primarily affects the estimated trend of a population. By weighting fishing efforts heavily, the population trend most closely resembles the fishery CPUE. The CPUE for crab pots depends not only on exploitable crab abundance, but also on many other factors, such as pot size, soak time, bait, tidal cycle, and vessel characteristics. Pot size is limited by regulations in Alaska and has not changed much over time. Soak time is probably the most important factor but generally is not collected for crab fisheries. Tidal information is available, but the relationship between tidal condition and CPUE may be too complex to be used for effort standardization. Vessel characteristics can be used to adjust for temporal changes in fleet composition, but Johnson (1991) found that vessel characteristics do not effect the relationship between crab density and CPUE for the Kodiak RKC fishery from 1969 to 1982. The CPUE defined as catch per pot lift, which is available for most crab fisheries in Alaska, could explain only partial variation in crab densities. Therefore, heavy weighting of fishing effort would distort the true trend of crab abundance, whereas without fishing effort information the abundances in recent years have tended to be over-estimated. An error-weighting factor of one generally gave a good fit for both RKC populations.

Red king crab tend to aggregate by forming pods much in the same way that some fishes form schools. When crab abundance decreases, the area of distribution shrinks, and crab density in the remaining area is still relatively high. The overall geographic distribution of Bristol Bay RKC has gradually shrunk since crab abundances peaked in the late 1970's. Such aggregate or schooling behavior may produce compensatory catchability (Clark, 1974). When population abundances are low, compensatory catchability

can easily result in overestimates of population abundances and overfishing if a constant catchability is assumed. On the other hand, when population abundances are high, abundances may be underestimated because of gear saturation (Bannerot and Austin, 1983). We modified Equation 10 in a manner described by Bannerot and Austin (1983) to compare the results between constant and density-dependent catchabilities. Overall, both relative and absolute abundances estimated under a constant catchability assumption fitted closer to the survey abundances for both populations than those fitted under an assumption of density-dependent catchability. It is conceivable that our fishery CPUE data may not have sufficient information to estimate density-dependent catchability.

As with conventional catch-age or cohort analyses, without auxiliary information there is great uncertainty in estimating the abundance in the terminal year by catch-length analyses. The accuracy of estimated absolute abundance in the terminal year depends on how accurately we can estimate fishing mortality. However, by incorporating fishing effort data, even with large measurement errors, it has been possible to estimate relative abundance trends rather well in most recent years. In cases where fishing effort is not available, an upper limit should be set for recruitment in the terminal year to avoid biasing the trend of relative abundances upward in the most recent years.

The selectivity coefficient for the first length class was estimated to be less than one for all scenarios; thus legal crabs with sizes close to the size limit appear to have a lower catchability. Legal male crabs have been mature for at least one or two years and theoretically should fully recruit to the fishing gear. But the observed catch-length frequency shows that length compositions of the first length class were smaller than those of the second length class for both fisheries and for all years except 1993. This selectivity may be partially caused by throwing back some barely legal-size crabs that were incorrectly measured by fishermen. The catch-length analysis may sometimes fail to estimate selectivity because selectivity coefficients and recruitment parameters may be confounded. A low proportion of recruitment to the first length class of new-shell crabs can cancel the effect of selectivity. We suggest that the selectivity coefficient for the first length class be interactively set to different values less than one during estimation until  $RSS$  cannot be further minimized. In recent years, observers have been placed on crab catcher and floater processors in Bristol Bay, and length frequency of the catch has been measured before sorting. In the future, comparison of the time series of length-frequency data on presorted and retained catches could

be used to estimate selectivity, and then selectivity could be fixed in catch-length analyses.

The trend of legal male abundances for Kodiak RKC is similar to that for Bristol Bay RKC, except that the Kodiak stock peaked 13 years prior to Bristol Bay. The high estimated abundance for the Kodiak population in the early 1960's may partly reflect expansion of the fleet to new fishing grounds (Spalinger<sup>5</sup>), whereas the peak abundance for the Bristol Bay population in the late 1970's resulted from strong recruitment (Zheng et al., 1995). Both populations decreased dramatically from their peak abundances within a few years and then fluctuated at low levels over time. When these two populations are examined over the same time scale, the trends are quite different. The abundance for the Bristol Bay population increased greatly from the early to late 1970's, whereas the abundance for the Kodiak population gradually decreased during the same period. The abundances for both populations decreased from 1980 to 1982. Since 1982 the Bristol Bay population has recovered a little, whereas the Kodiak population has completely collapsed and has not been able to support a fishery (Spalinger<sup>5</sup>).

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