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[Article]

Analysis of a Stock–Recruit Relationship for Red King Crab off Kodiak Island, Alaska

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Abstract.—Waters of the northern Gulf of Alaska around Kodiak Island once supported the world's largest fishery for the red king crab *Paralithodes camtschaticus*. Commercial fisheries began at low levels in the 1930s, increasing rapidly in the 1960s to a peak harvest of 42,800 metric tons in 1965. Stock abundance declined sharply in the late 1960s, moderated in the 1970s, and crashed in the early 1980s. A commercial fishery closure since 1983 has not resulted in stock recovery. To improve understanding of stock dynamics, we examined spawner–recruit (S-R) relationships for the Kodiak red king crab stock. The shape of the S-R relationship helps describe average stock productivity at different stock levels, thus relating directly to fishery management objectives. Due to limited female data, we used only male data and two currencies of male abundance as a proxy for spawners: either (1) all males greater than or equal to 125 mm carapace length (CL) or (2) legal males ($\geq$145 mm CL). Due to age uncertainty, we considered lag times of 5 to 8 years between reproduction and recruitment. Residuals from fitting a standard Ricker model were strongly negative for brood years from the mid-1970s to the mid-1980s and positive from the early to mid-1990s. A Ricker model with autocorrelated errors resulted in better fits with corrected Akaike's information criterion (AIC_c) values minimized for a 5-year lag using all males. Among model configurations, estimates of peak production ranged from 2.0 to 3.4 million recruits from a range of 11.3 to 37.7 million males. A model separating the time series into three productivity periods corresponding to different ecological regimes further improved model fit. Although abundances of both spawners and recruits have been less than 1.0 million males since 1985, depensation at low stock sizes was not detected. Future analyses will examine the contribution of ecological and environmental factors to crab recruitment.

The northern Gulf of Alaska near Kodiak Island (Figure 1) once supported the world's largest fishery for the red king crab *Paralithodes camtschaticus*. Commercial harvests from this area first occurred in the 1930s, although annual harvests were relatively minor until the early 1960s when improved market conditions, changes in vessel technology, and the introduction of vessels designed specifically to harvest red king crab resulted in a rapid increase in fishing effort and catch (Figure 2; Gray et al. 1965; Spalinger 1992). Annual landings peaked at 42,800 metric tons (94.4 million pounds) in 1965, but despite much lower harvest levels in the 1970s (Figure 2; Spalinger and Jackson 1994), the population collapsed in 1982 (Table 1). A fishery closure in place since 1983 has failed to induce stock recovery.

Recruitment is the primary determinant of dynamics of Alaskan crab populations (Zheng and Kruse 2000). To improve understanding of the role of population dynamics on the collapse and failure to recover of the Kodiak red king crab population, the goal of this study was to develop a spawner–recruit (S-R) relationship for this stock. The shape of the S-R relationship, which is a primary factor in determining average productivity at different stock levels, is an indicator of the potential role of recruitment overfishing on stock collapse and failure to recover and, thus, relates directly to fishery management objectives and the choice of harvest strategies to maintain a target level of stock production in the future.

Under the simplest approach, the S-R model assumes recruitment is related to stock biomass at low biomass levels, but density-dependent factors limit recruitment at high levels of stock abundance (Ricker 1975; Hilborn and Walters 1992; Quinn and Deriso 1999). In such cases, mortality during early life increases with increasing stock size because survival becomes constrained by density dependence involving food, space, suitable habitat, or predators (Ricker 1954; Beverton and Holt 1957). If the early life stages are self-limiting, as might occur with competition for food or space, the S-R relationship might be described by a Beverton–Holt model, which approaches an asymptotic level of recruitment as stock abundance increases (Beverton and Holt 1957). In the Beverton–Holt model, compensation is assumed to occur throughout the range of stock sizes. However, many fished stocks

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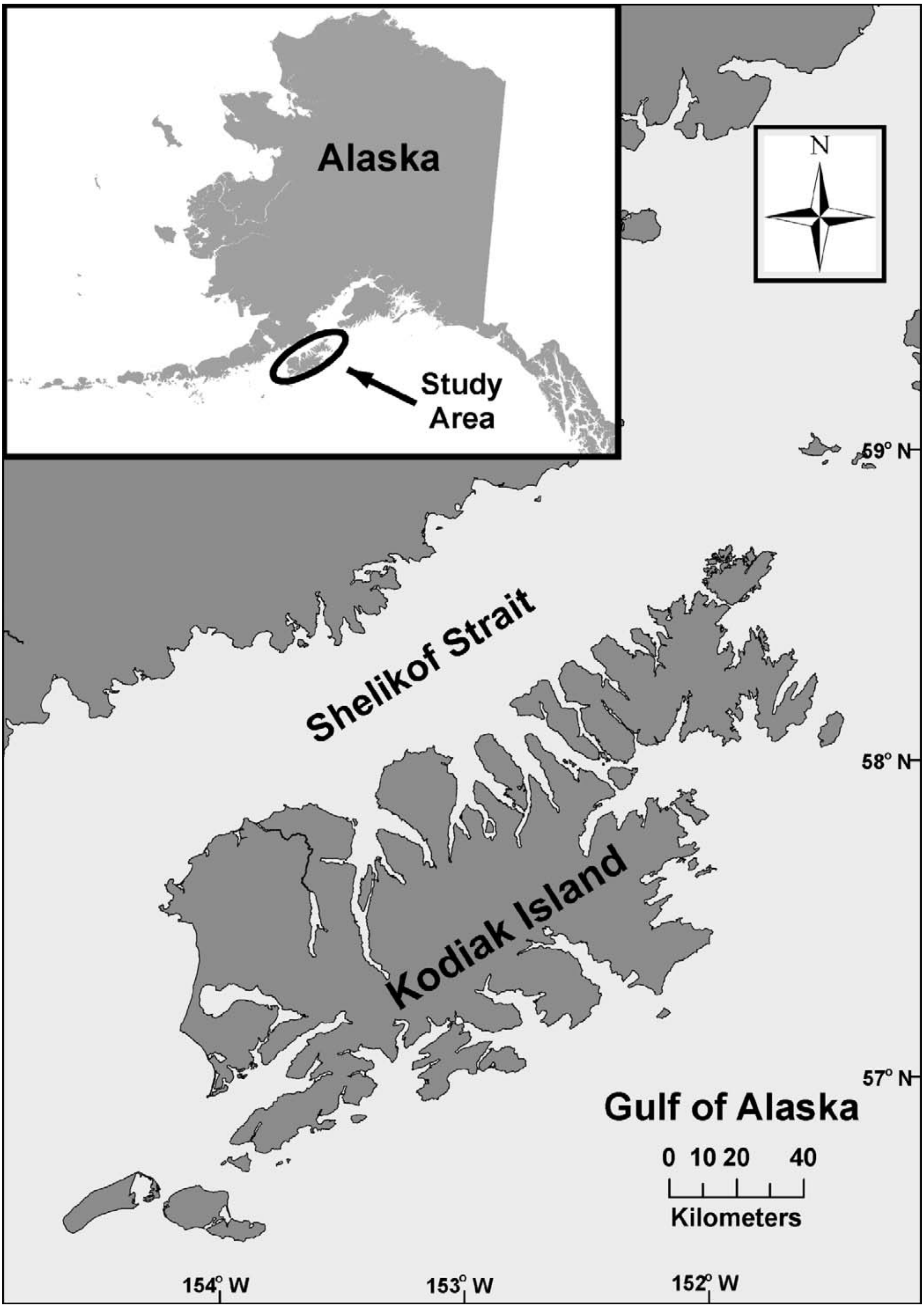

FIGURE 1.—Study area around Kodiak Island, Alaska.

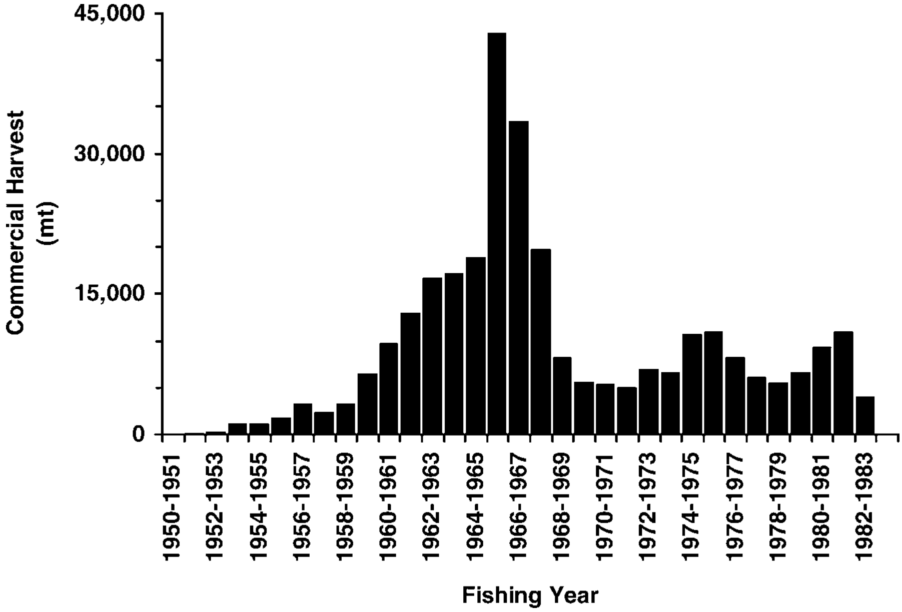

FIGURE 2.—Annual harvests (metric tons [mt]) of red king crab from the Kodiak Management Area, Alaska, during 1950 to 1982.

exhibit overcompensation in which recruitment, representing spawning success over all life stages from reproduction to the recruit stage, is a dome-shaped function that decreases as stock size increases beyond a peak production level, as in the Ricker S-R model.

Another consideration in S-R models is depensation, whereby per capita production decreases disproportionately as stock size decreases at very low stock levels. Depensation may result from several sources, including reduced probability of fertilization, impaired group dynamics, reduced ability to condition the environment, or predator saturation (Allee et al. 1949; Liermann and Hilborn 2001). As an extension of this mechanism, population abundance may stabilize around a relatively low equilibrium or predator pit (Peterman 1977).

The goal of our study was to determine if there is a biologically meaningful S-R relationship for Kodiak red king crab. Several Ricker S-R relationships warrant investigation. We first fitted the standard Ricker S-R relationship in which sequential observations are assumed to be independent and uncorrelated. However, the autocorrelated environmental factors influencing crab recruitment may lead to strong serial correlation in recruitment such that good years tend to follow good years and poor years follow poor years (Quinn et al. 1990; Hare and Mantua 2000). A second possibility is the autocorrelated Ricker model was fitted with errors in the S-R relationship that are serially correlated. A third possibility, depensatory population dynamics (Quinn and Deriso 1999; Liermann and Hilborn 2001), may explain the continued low levels of abundance and recruitment for the Kodiak red king crab population beginning in the early 1980s. We examined the potential of depensation by considering a gamma model, a three-parameter generalization of the Ricker model (Reish et al. 1985). Zheng et al. (1995a, 1995b) similarly used depensatory and autocorrelated Ricker models to explore S-R relationships for Bristol Bay red king crab. The Bristol Bay models used female data from 1968 to the mid-1990s for recruitment and spawner biomass but with spawners constrained by male reproductive potential. Subsequently, the S-R analysis for Bristol Bay was updated with a recruitment time series extending to 2001 (Zheng and Kruse 2003). Results of these efforts suggested an autocorrelated Ricker model provided the best fit, although only marginally better than the depensatory model. Also, observed recruitment trends were consistent with decadal-scale climate shifts.

Because a lack of age structures prevents accurate age estimation of red king crab, the time lag between mating and subsequent model recruitment (specified below) must be specified. The consequence of uncertainty in this assumption was investigated by sensitivity analysis by means of a range of plausible time lags.

Methods

In a recent retrospective analysis (Bechtol and Kruse, in press), we included data from dockside samples of commercial harvests (1960–1982) and indices of stock composition and relative abundance from pot (1972–1986) and bottom trawl surveys (1986–2004) in a catch survey analysis to yield estimates of crab abundance and recruitment. To maximize the available data for an S-R relationship, we limited our analysis to males because (1) this is a male-only fishery (Pengilly and Schmidt 1995), so female abundance estimates were limited to survey years (1972–2004), whereas male estimates extended from 1960 to 2004 owing to availability of male commercial catch data; and (2) the years of the highest population abundance, particularly the 1960s, are represented only by male data. Moreover, for consistency, male data were the basis of a recent analysis of S-R relationships for crabs in the eastern Bering Sea for purposes of revising overfishing definitions (NPFMC 2007).

In our previous analysis, we defined three "stages" or classes of male crab: prelegal, legal recruit, and postrecruit (Bechtol and Kruse, in press). The minimum size limit for legal retention of male red king crab for most years in the Kodiak Management Area was 178 mm carapace width, equivalent to approximately 145 mm carapace length (CL; Blau 1988). The growth increment of adult males at this size is approximately 20 mm CL (McCaughran and Powell 1977). We defined legal recruits as newshell males that were greater than or equal to 145 mm CL and less than 165 mm CL (i.e., determined to have molted to a legal size within the previous year). Postrecruit males were defined as having been legal size for at least 1 year and included oldshell and very oldshell males that were greater than or equal to 145 mm CL and less than 165 mm CL, plus all males that were greater than or equal to 165 mm CL regardless of shell condition. Prelegal crab are considered to be one molt smaller than legal size and were defined as males of any shell condition that were greater than or equal to 125 mm CL and less than 145 mm CL. Given the available data, we defined recruitment as the number of crab in the prelegal stage entering the modeled population rather than those entering the fishery or to some earlier life stage (e.g., larval settlement into the benthos).

TABLE 1.—Annual estimated red king crab abundances (thousands of crab) of male recruits, legal males, and all males of the Kodiak, Alaska, stock, 1960 to 2004 (from Bechtol and Kruse, in press). Male recruits are new recruits greater than or equal to 125 and less than 145 mm carapace length (CL), legal males are greater than or equal to 145 mm CL, and all males include all crab greater than or equal to 125 mm CL (see Bechtol and Kruse, in press, for details).

Year	Male recruits	Legal males	All males
1960	5,287	11,456	16,743
1961	20,906	10,799	32,368
1962	31,641	17,415	51,435
1963	25,101	25,246	53,761
1964	13,226	31,176	47,523
1965	7,190	28,797	37,901
1966	3,947	17,552	22,500
1967	5,634	8,453	14,586
1968	4,255	5,662	10,508
1969	2,737	4,565	7,785
1970	6,208	3,628	10,171
1971	3,808	5,127	9,635
1972	2,735	5,696	8,980
1973	5,684	6,015	12,155
1974	5,903	8,458	15,220
1975	3,072	8,947	12,913
1976	902	7,930	9,371
1977	3,643	5,925	9,766
1978	12,469	4,646	17,481
1979	8,661	7,162	16,863
1980	2,033	8,575	11,615
1981	1,076	7,529	8,980
1982	747	1,552	2,394
1983	531	718	1,343
1984	156	940	1,173
1985	67	621	709
1986	24	474	509
1987	33	455	493
1988	12	440	458
1989	16	411	430
1990	191	210	403
1991	166	238	424
1992	90	97	194
1993	37	80	124
1994	84	89	178
1995	149	51	204
1996	227	162	412
1997	5	334	375
1998	78	229	311
1999	162	199	370
2000	332	105	445
2001	147	183	357
2002	106	109	224
2003	102	69	176
2004	152	144	312

In the Kodiak area, the male size at physiological maturity (75–85 mm CL), the size at which sperm are produced, is smaller than the size at functional maturity (≥125 mm CL), the size at which males have been observed in mating pairs. Mean age for male functional maturity is 7 to 8 years (McCaughran and Powell 1977). Male crab can copulate with multiple females during the mating season, but laboratory studies found reduced fertilization success associated with smaller males and with secondary or later matings by a given male (Paul and Paul 1990, 1997). In the wild, mating success with multiple females may be further constrained by factors such as the availability of mates, duration of premating and postmating male attendance, synchrony of female molting, and the relatively short duration of the mating season. Thus, there is much uncertainty concerning the component of the assessed male population in a given year that may have contributed to future recruitment. Given this uncertainty, we examined the sensitivity of our assumptions about the reproducing male population in two ways.

First, we considered plausible time lags ranging from 5 to 8 years between the year of reproduction, or brood year, and the year of recruitment to the assessment model. Second, we examined two definitions of the reproducing male population which we define as "currencies." This approach was needed because in contrast to the crab fishery, which is managed based on a knife-edged delineation of legal size, sexual maturation in male red king crab occurs across a relatively broad range of sizes. However, the contribution of different size components of the male population to reproductive success varies according to the size composition of the female component of the population (Paul and Paul 1990, 1997; Kruse 1993); the relative male and female compositions change according to year-class strength due to differential male and female growth rates (McCaughran and Powell 1977). To address uncertainty in male reproductive contribution across long-term population patterns, we considered male spawner currencies as including either (1) all male crab greater than or equal to 125 mm CL; or (2) only the legal recruit and postlegal stages (i.e., males greater than or equal to 145 mm CL).

The relationship between recruitment and the estimated reproductive stock abundance was examined with the Ricker model (Ricker 1954),

$$R_t = \alpha S_{t-k} e^{-\beta S_{t-k} + \nu_t}, \tag{1}$$

where α is a productivity parameter representing production at low stock size, β is a parameter controlling the degree of density dependence, R is recruit abundance in year t, and S is stock size lagged k years from year t. By letting $\nu_t = \delta_t + \varphi\nu_{t-1}$, where δ_t is environmental white noise assumed to be distributed as $N(0,\ \sigma^2)$, equation (1) incorporates autocorrelation effects with φ representing the degree of autocorrelation among residuals in the predicted relationship. Setting $\varphi = 0$ results in the standard Ricker model. The depensatory model is given by:

$$R_t = \alpha S_{t-k}^{\gamma} e^{-\beta S_{t-k} + \nu_t} = \alpha S_{t-k}(S_{t-k}^{\gamma-1} e^{-\beta S_{t-k} + \nu_t}), \tag{2}$$

where a value of γ greater than 1 suggests depensation and other parameters are as in equation (1), including configurations with and without autocorrelation (Reish et al. 1985; Quinn and Deriso 1999).

These equations were linearized by taking logarithms:

$$\begin{aligned} \log_e\left(\frac{R_t}{S_{t-k}}\right) &= \log_e(\alpha) - \beta S_{t-k} + \nu_t \\ \log_e\left(\frac{R_t}{S_{t-k}}\right) &= \log_e(\alpha) + (\gamma - 1)\log_e(S_{t-k}) \\ &\quad -\beta S_{t-k} + \nu_t. \end{aligned} \tag{3}$$

Peak recruitment in the Ricker model occurs at a stock size (S_p) of $1/\beta$ and in the depensatory model at a stock level of γ/β, provided that γ is greater than 0 and β is greater than 0. The presence of autocorrelation was tested by calculating the lag-1 Pearson correlation of the residuals from the model and applying the standard hypothesis test of zero correlation (Zar 1999). Per-capita productivity and depensation among competing models was compared by means of α and β, respectively, divided by peak spawner abundance (S_p), so that comparisons between the two male currencies could be made.

To explore whether there were climate regime changes in the S-R parameters, we further evaluated our optimal model(s) by means of configurations with up to three of each of the α and β parameters across the 45-year time series. The sequence of years chosen for a given α and β parameter combination was examined through trial and error by iteratively adjusting the transition points but beginning with those years that were previously identified as being ecosystem regime shifts (Hare and Mantua 2000; Peterman et al. 2000).

These models were implemented in AD Model Builder (Otter Research, Sidney, British Columbia, Canada), with additional validation by means of Microsoft Excel (Microsoft Corporation, Redmond, Washington). Relative precision of an estimated parameter was reported as the coefficient of variation (CV), the standard error (obtained in AD Model Builder) divided by the estimate.

In addition to visual examination of residual patterns, our approach to model selection involved comparing values of the corrected Akaike's information criterion (AIC$_c$; Burnham and Anderson 2004):

$$\begin{aligned} \hat{\sigma} &= \sqrt{\frac{\mathrm{RSS}}{n-p}} \\ -2\log_e L &= n\log_e(2\pi\hat{\sigma}^2) + \frac{\mathrm{RSS}}{\hat{\sigma}^2} \\ \mathrm{AIC}_c &= -2\log_e L + 2p + \frac{2p(p+1)}{n-p-1}, \end{aligned} \tag{4}$$

where n is the number of observations, RSS is the residual sums of squares, p is the number of parameters in the model, and AIC$_c$ is a formulation of Akaike's information criterion corrected to accommodate small sample sizes (n). According to Burnham and Anderson (2004), AIC$_c$ differences of less than 2 indicate that there is no credible evidence to eliminate competing models; AIC$_c$ differences of 2 to 4 indicate that there is weak evidence for elimination; and differences above 4 indicate that there is definite evidence. To provide comparable results among configurations, recruit abundances resulting from the 1960 to 1996 brood

TABLE 2.—Parameter estimates and their coefficients of variation, and corresponding estimates of peak abundances of red king crab male spawners and model recruits for the standard Ricker and autocorrelated Ricker models. The number in the model name identifies the lag in years between brood year and model recruitment (A = all males; L = legal males only; Est. = the parameter estimate; CV = the coefficient of variation of the estimate; NA = not applicable).

	Parameter estimates and standard deviations						Peak abundances ($\times$ 1,000 crab)	
	α		β		φ			
Model	Est.	CV	Est.	CV	Est.	CV	Spawners	Recruits
Standard Ricker model								
5L	0.26	0.15	2.3×10^{-5}	0.64	NA	NA	44,016	4,209
6L	0.24	0.15	2.9×10^{-5}	0.39	NA	NA	34,256	3,052
7L	0.23	0.15	3.6×10^{-5}	0.41	NA	NA	28,140	2,369
8L	0.22	0.15	4.1×10^{-5}	0.35	NA	NA	24,237	1,923
5A	0.15	0.15	1.2×10^{-5}	0.65	NA	NA	81,273	4,503
6A	0.14	0.15	1.8×10^{-5}	0.45	NA	NA	56,959	3,001
7A	0.14	0.15	2.2×10^{-5}	0.37	NA	NA	46,445	2,325
8A	0.13	0.15	2.4×10^{-5}	0.34	NA	NA	42,355	1,972
Autocorrelated Ricker model								
5L	0.49	0.52	6.3×10^{-5}	0.53	0.75	0.10	15,939	2,890
6L	0.39	0.50	6.1×10^{-5}	0.54	0.76	0.09	16,499	2,350
7L	0.54	0.64	7.9×10^{-5}	0.43	0.82	0.08	12,589	2,498
8L	0.48	0.58	8.9×10^{-5}	0.38	0.80	0.08	11,263	1,988
5A	0.24	0.48	2.7×10^{-5}	0.70	0.73	0.11	37,726	3,354
6A	0.23	0.48	3.8×10^{-5}	0.50	0.75	0.09	26,361	2,222
7A	0.30	0.59	4.9×10^{-5}	0.40	0.80	0.09	20,205	2,258
8A	0.25	0.56	4.2×10^{-5}	0.46	0.80	0.08	23,871	2,154

years were examined, giving 37 observations (*n*) for reproduction-to-recruitment lags of 5 to 8 years.

Several alternative models were also examined, including the Beverton–Holt (Beverton and Holt 1957), Ludwig–Walters (Ludwig and Walters 1989), Deriso–Schnute (Deriso 1980; Schnute 1985), and Shepherd (Shepherd 1982) models. Results of the Beverton–Holt model were similar to the results of the Ricker model and are not presented. The other models were less parsimonious based on AIC_c values and residual patterns and are excluded from further discussion.

Results

Estimated recruitment abundance was highly variable over time (Table 1; Bechtol and Kruse, in press), with a ratio of strongest to weakest recruitments of 6,328 (31.6 million male crab in 1962 versus 5,000 male crab in 1988). However, given the time lag between mating and recruitment, the S-R analysis excluded the years of highest recruitment in the early 1960s because stock abundance estimates were not available for the associated brood years in the 1950s. Within the range of recruitments beginning in 1965, giving a minimum lag of 5 years, corresponding to the smallest lag reported here, the ratio became 2,494 between the strongest (12.5 million males in 1978) and weakest (5,000 males in 1988) recruitments. Observed recruitment was highest in the 1960s, moderate in the late 1960s and 1970s, and weak from the mid-1980s to the present (Table 1). Years of high recruitment were associated with moderate to high spawning stock abundances in the 1960s and early 1970s, whereas both recruitment and estimated male reproductive abundance have remained low since 1982.

Estimated peak recruitment among standard Ricker curves ranged from 1.9 to 4.5 million male crab (Table 2). Peak recruitment was inversely related to the lag length between brood year and recruitment. Spawner abundance corresponding with peak recruitment ranged from 24.2 to 44.0 million crab if measured as legal males ($\geq$145 mm CL) or 42.4 to 81.3 million crab if measured as all males ($\geq$125 mm CL; Table 2). However, this spawner abundance level is well beyond the observations for all brood years (Figure 3A, C, E, G). The S-R relationships for brood years after 1982 reveal a very different relationship between recruitment and spawner abundance owing to the sharp reduction in male abundance and recruitment levels beginning in the early 1980s (Figure 4). Estimates of α and β were larger for legal-male models than for all-male models under similar lags and correlation configurations (including for autocorrelated models discussed below), although the precision of the estimates was similar for a given configuration (Table 2). For all lag times examined with the standard Ricker models, residuals were distributed around zero during the 1960s, moderately to strongly positive during the early

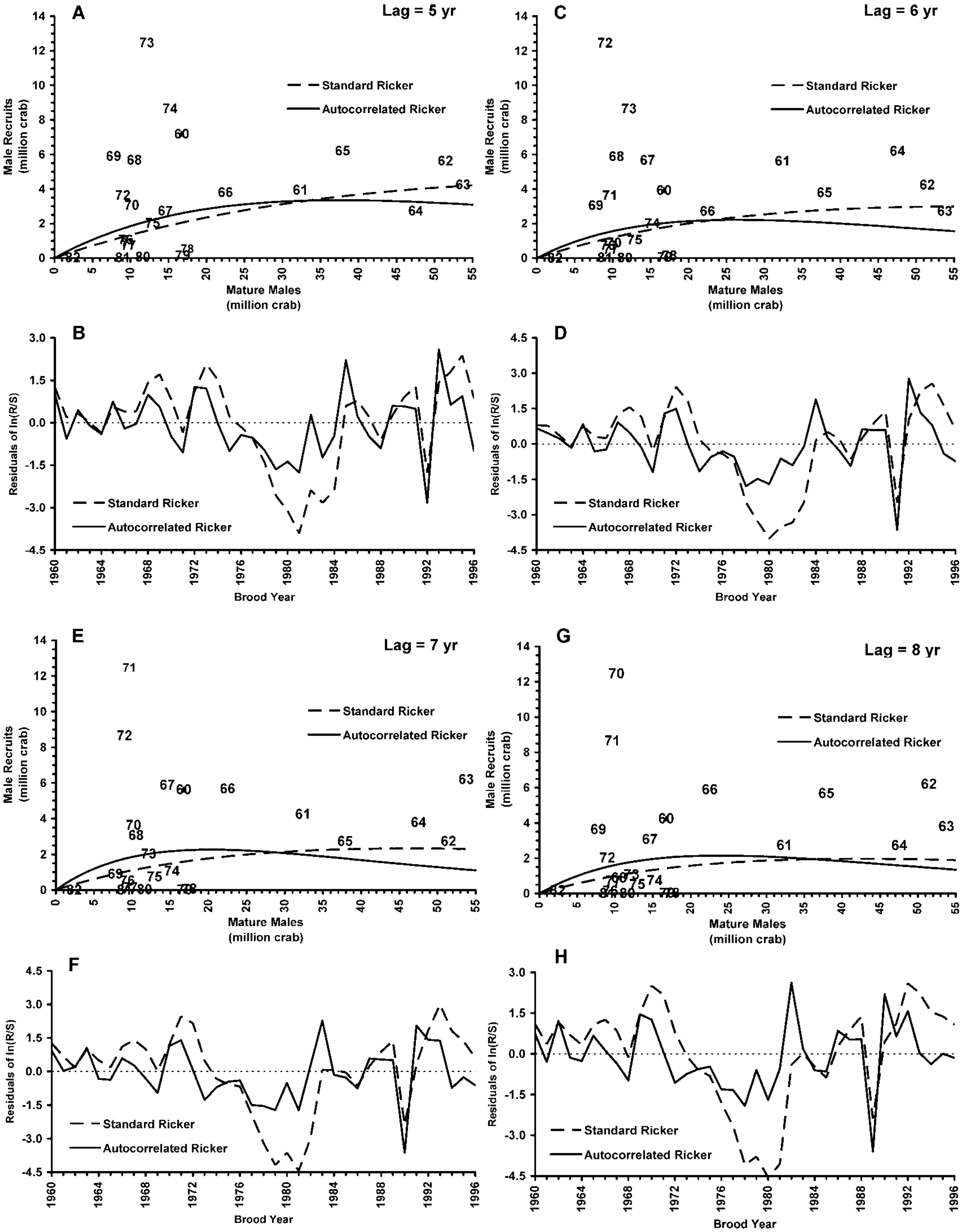

FIGURE 3.—Standard Ricker (dashed line) and autocorrelated Ricker (solid line) curves with 5- to 8-year lags, showing the relation between abundance of red king crab male recruits (R) and abundance of all mature males (stock size [S]; upper panels), and prediction residuals of $\log_e(R/S)$ by brood year (lower panels) for the 1960 to 1996 brood years. Numerical labels on upper panels indicate the 1960 to 1996 brood years.

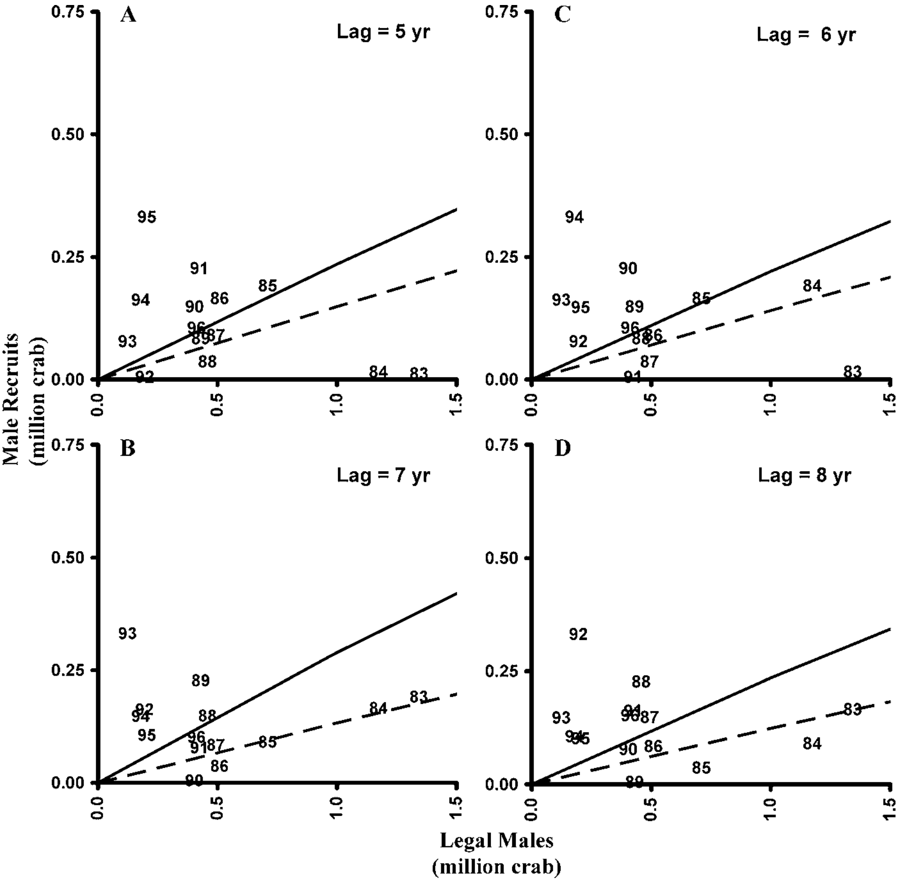

FIGURE 4.—Origin area of the standard Ricker (dashed line) and autocorrelated Ricker (solid line) curves with 5- to 8-year lags, showing the relation between abundance of red king crab male recruits and abundance of all legal males for brood years after 1982. Numerical labels indicate brood years.

1970s and mid-1990s, and strongly negative from the late 1970s to early 1980s (Figure 3B, D, F, H). All models showed a strongly negative residual associated with the 1997 recruits, regardless of the brood year. Model fit, indicated by larger AIC_c values, generally decreased with longer recruitment lags, and fits were better for an all-male currency compared to a legal-male currency. Among standard Ricker models, the optimal configuration was a 5-year lag using an all-male currency based on an AIC_c value of 141.5 (Table 3).

Results of the test of serial correlation were highly significant ($P < 0.01$) for the model residuals from all standard Ricker models but not significant for residuals from all autocorrelated Ricker models (results not tabulated). A similar result was obtained for the depensatory models with and without an autocorrelation parameter. This indicates a bias in the results of the standard models because the assumption that data are uncorrelated is violated. The autocorrelation parameter corrects this bias.

For a given male currency and recruitment lag, incorporation of autocorrelation into the Ricker models reduced the spawner abundance estimated to produce peak recruitment (Table 2; Figure 3A, C, E, G). Peak recruitment under the autocorrelated Ricker model ranged from 2.0 to 3.4 million males resulting from a range in spawner abundance of 11.3 to 16.5 million crab if measured as legal males or 20.2 to 37.7 million crab if measured as all males (Table 2). The autocorrelated models had higher per-capita productivity (α/S_p) and greater density dependence (β/S_p) than comparable standard Ricker models (Table 3). As a result, the autocorrelated models estimated greater productivity than the standard Ricker models at low to moderate spawner abundances (Figure 3A, C, E, G; Figure 4). However, there was greater uncertainty in the estimated parameters for the autocorrelated Ricker

TABLE 3.—Numbers of parameters, estimated residual sum of squares (RSS), corrected Akaike's information criterion (AIC$_c$), and per-capita productivity values for each configuration of the standard Ricker and autocorrelated Ricker models of red king crab recruitment. The number in the model name identifies the lag in years between brood year and model recruitment (A = all males; L = legal males only; α = the productivity; β = density dependence; S_p = peak spawner abundance).

Model	p	RSS	AIC$_c$	α/S_p	β/S_p
Standard Ricker model					
5L	2	98.4	145.6	5.9×10^{-6}	5.2×10^{-10}
6L	2	106.8	148.6	1.0×10^{-5}	1.4×10^{-9}
7L	2	124.9	154.4	8.1×10^{-6}	1.3×10^{-9}
8L	2	137.6	158.0	8.9×10^{-6}	1.7×10^{-9}
5A	2	88.0	141.5	1.9×10^{-6}	1.5×10^{-10}
6A	2	106.8	148.6	2.5×10^{-6}	3.1×10^{-10}
7A	2	120.5	153.1	2.9×10^{-6}	4.6×10^{-10}
8A	2	128.8	155.6	3.0×10^{-6}	5.6×10^{-10}
Autocorrelated Ricker model					
5L	3	46.6	120.4	3.1×10^{-5}	3.9×10^{-9}
6L	3	49.2	122.4	2.3×10^{-5}	3.7×10^{-9}
7L	3	46.8	120.5	4.3×10^{-5}	6.3×10^{-9}
8L	3	55.0	126.5	4.3×10^{-5}	7.9×10^{-9}
5A	3	43.7	118.0	6.4×10^{-6}	7.0×10^{-10}
6A	3	49.1	122.4	8.7×10^{-6}	1.4×10^{-9}
7A	3	49.2	122.4	1.5×10^{-5}	2.4×10^{-9}
8A	3	50.2	123.2	1.0×10^{-5}	1.8×10^{-9}

models (CVs ranged from 0.48 to 0.64 for α and from 0.38 to 0.70 for β) relative to the estimates for the standard Ricker models (the CV was 0.15 for α and from 0.34 to 0.65 for β). Improved model fit, as indicated by smaller AIC$_c$ values, was obtained for the autocorrelated Ricker models compared to the standard Ricker models (Table 3). Improved model fit for all-male currencies was less pronounced for the autocorrelated models with longer recruitment lags. Residuals were generally smaller (i.e., closer to 0) for the autocorrelated Ricker model compared to the standard Ricker model during many years, particularly years in which the largest residuals were observed, such as during the late 1970s to early 1980s (Figure 3B, D, F, H). Despite the brood year, all autocorrelated Ricker model lags also showed a strongly negative residual associated with the 1997 recruits and a strong positive residual associated with the 1990 recruits. Within the autocorrelated Ricker configurations, a 5-year recruitment lag using all males provided the best model with an AIC$_c$ value of 118.0. Nevertheless, there is only weak evidence (i.e., $2 \leq$ AIC$_c$ difference ≤ 4) that this model is better than the autocorrelated Ricker models with 5- and 7-year lags using legal males (AIC$_c$ values of 120.4 and 120.5, respectively).

For most configurations, the depensatory models had difficulty converging to realistic results. Constraining β to be nominally positive (i.e., $>1.0 \times 10^{-7}$) improved model convergence, but model plots of residuals showed little improvement and AIC$_c$ values indicated less parsimony compared to autocorrelated Ricker configurations. The only exception was a lag-5 autocorrelated depensatory model that readily converged and produced an AIC$_c$ value of 119.1 (data not tabulated), suggesting no credible difference (i.e., AIC$_c$ difference ≤ 2) from the lag-5 autocorrelated Ricker model (AIC$_c$ value of 118.0; Table 3). However, the predicted values for the lag-5 autocorrelated depensatory model indicated overcompensation at spawner values much larger than observed abundances, and peak spawner abundance of 71.5 million males seemed unrealistic compared to either the standard or autocorrelated Ricker models. We concluded that depensation is not indicated in these S-R models for red king crab.

Given that only weak difference as the best model exists among autocorrelated Ricker models (lag-5 or lag-7 with legal males or lag-5 with all males), these autocorrelated models were re-examined with up to three α or β parameters or both. The optimal sequence of years varied with lag length and male currency. Configurations considering two periods were best represented with brood year periods of 1960 to 1974 and 1975 to 1999 for lag-5 models and periods of 1960 to 1972 and 1973 to 1997 for lag-7 models. Three periods were best represented by brood year groupings of 1960 to 1974, 1975 to 1984, and 1985 to 1999 for lag-5 models and 1960 to 1972, 1973 to 1986, and 1987 to 1999 for lag-7 models. The smallest AIC$_c$ value of 109.0 occurred for a lag-5 autocorrelated all-male Ricker model with three α and one β parameters (Table 4; Figure 5). The second best model, with an AIC$_c$ value of 113.3, was a lag-5 autocorrelated Ricker model with legal males (Table 4). Under the criterion of Burnham and Anderson (2004), this all-male configuration substantially improved model fit, as indicated by AIC_c value differences larger than 4, over alternative autocorrelated Ricker models with either single or multiple α and β parameters (Tables 4, 5). We note that all models with three β parameters failed to converge without severely bounding the β parameters.

As a generalization, incorporation of multiple α parameters in model configurations resulted in greater productivity (larger estimated α) and, conversely, multiple β parameters resulted in reduced density dependence (smaller β), during the early portion of the time series relative to a single α or β, respectively, for the entire time series. This is exemplified by a lag-5 autocorrelated Ricker model based on all males and estimating three α and one β parameters (Figure 5A). In the configuration with a single α parameter, peak recruitment of 3.4 million males corresponds with peak spawner abundance of 37.7 million males (Table 2). In contrast, the best model in which the time series is partitioned into three periods represented by different α parameters and a single β parameter shows substantially different productivity among brood year groupings. Although peak recruitment for all periods occurs from 32.8 million spawning males (defined as 1/β), the magnitude of recruitment varies among the three periods. For the first period, encompassing the 1960 to 1974 brood years, estimated peak recruitment is 5.3 million crab ($\alpha = 0.44$) and is noticeably higher (Figure 5B) compared to the single α model. Per-capita productivity during this first period is 1.4×10^{-5}. In the second period ($\alpha = 0.03$), the 1975 to 1984 brood years, the same level of peak male spawners results in a peak recruitment of only 0.4 million males and per-capita productivity is 8.9×10^{-7}. The final period, representing the 1985 to 1996 brood years ($\alpha = 0.32$), results in peak recruitment of 3.9 million males with per-capita productivity of 9.8×10^{-6}. Examination of residual patterns indicates improved model fit in the 1978 to 1996 brood years but with only incremental improvement at best through the remainder of the time series (Figure 5C). Based on AIC_c value and the corresponding indication that S-R parameters changed over the time period, the optimal model becomes the lag-5 autocorrelated Ricker model with three α parameters and a single β parameter for the entire time series.

TABLE 4.—Corrected Akaike's information criterion (AIC_c) values from different configurations of an autocorrelated Ricker model of red king crab recruitment, lagged by 5 and 7 years (legal males) or 5 years (all males); the time series is divided into up to three different segments, indicated by α and β quantities of 1–3.

Number of β parameters	Number of α		
	1	2	3
	Lag-5 using legal males		
1	120.4	119.0	113.3
2	117.5	119.8	116.3[a]
3	119.8[a]	122.4[a]	118.4[a]
	Lag-7 using legal males		
1	120.5	119.6	120.1
2	117.3	119.6	121.3
3	119.9[a]	122.4[a]	124.6[a]
	Lag-5 using all males		
1	118.0	116.8	109.0
2	117.1	118.7	111.5[a]
3	119.8[a]	121.6[a]	122.0[a]

[a] Values for β were constrained to force model convergence.

Discussion

Several studies have investigated S-R relationships for red king crab in Alaska (Reeves 1990; Greenberg et al. 1991; Zheng et al. 1995a, 1995b; Zheng and Kruse 2003), but there are few published analyses of S-R relationships for red king crab in the Gulf of Alaska. Schmidt et al. (1992) considered a variety of potential factors contributing to Kodiak red king crab stock–recruitment but concluded the time series of survey data were insufficient to draw conclusions about the effect of adult females on subsequent age-5 male recruitment. Zheng et al. (1995a, 1995b) and Zheng and Kruse (2003) developed S-R relationships for red king crab in Bristol Bay, Alaska, based on effective spawning biomass, determined as a function of mature females relative to functionally mature males. The Bristol Bay analyses (Zheng et al. 1995a, 1995b; Zheng and Kruse 2003) found that an autocorrelated Ricker model provided a slightly better fit than a depensatory model because years of strong and weak recruitment occurred over separate periods (Zheng et al. 1995a).

Our Kodiak study similarly found that autocorrelated models provided better fits than other models considered (Figure 3B, D, F, H), with notable improvement during periods of negative residuals in the late 1970s to early 1980s and positive residuals in the 1990s (Figure 5C). Patterns near the origin further suggest autocorrelation with one series of brood years (the mid- to late 1980s) with weak recruitment, followed by a second series of brood years (early 1990s) in which recruitment was still weak but slightly better than the late 1980s (Figures 4A, 5B). Our optimal model using all males in a lag-5 configuration with three α parameters to accommodate different productivity for brood years 1960 to 1974, 1975 to 1984, and 1985 to 1996 reduced overall autocorrelation across the time series to a φ of 0.44 (Table 5), smaller than the 0.66 value found by Zheng et al. (1995a) for male red king crab in Bristol

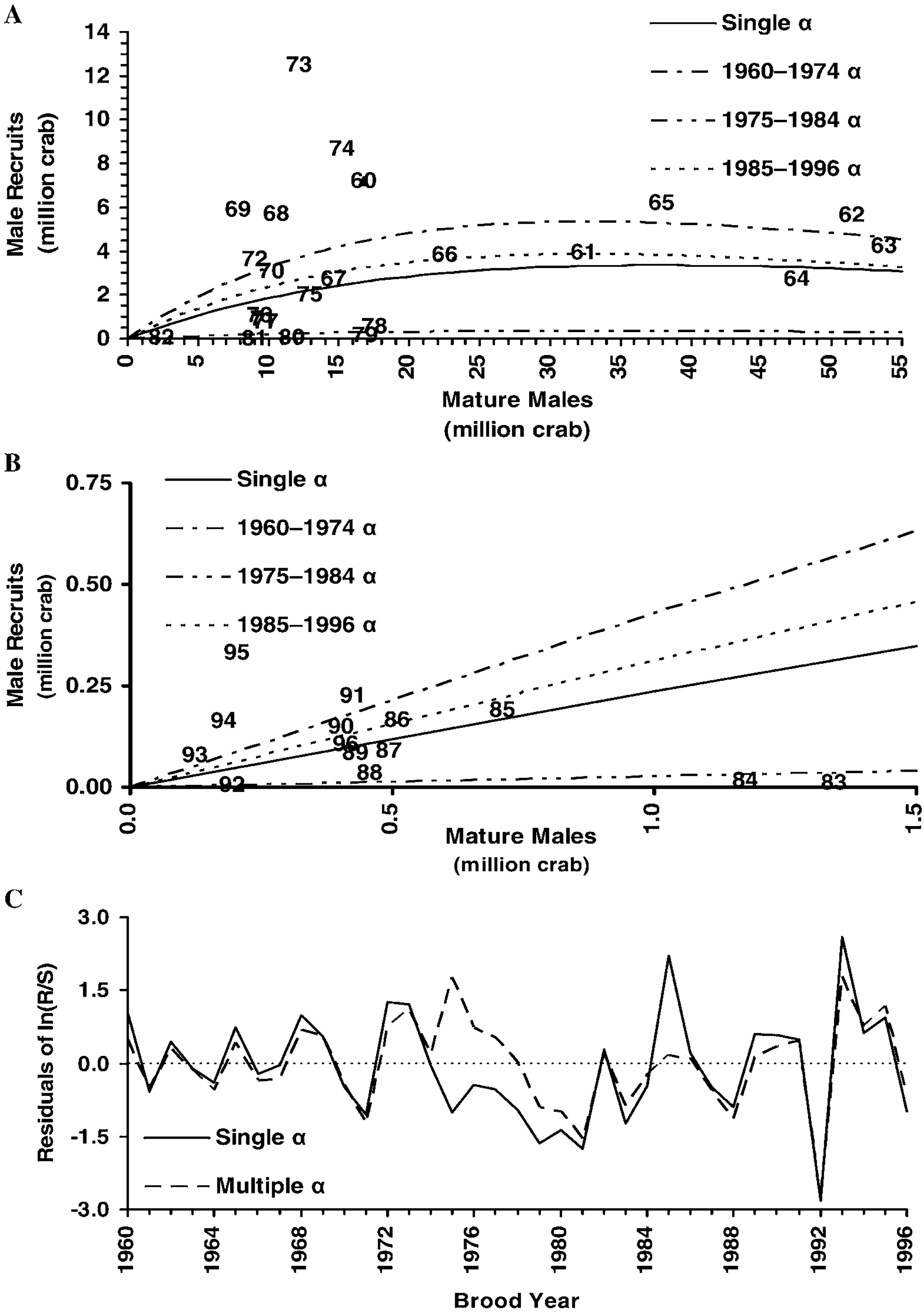

FIGURE 5.—Lag-5 autocorrelated Ricker curves illustrating the relation between abundance of red king crab male recruits (R) and abundance of all mature males (stock size [S]) and comparing a single α parameter for all brood years versus three separate α parameters (i.e., for the 1960 to 1974, 1975 to 1984, and 1985 to 1996 brood years): (**A**) curves for the entire time series; (**B**) the origins of curves; and (**C**) pattern of residuals of $\log_e(R/S)$. Numerical labels in panels (A) and (B) indicate brood years.

TABLE 5.—Parameter estimates (Est.) and corresponding coefficients of variation (CV), residual sum of squares (RSS) values, and corrected Akaike's information criterion (AIC_c) values for selected lag-5 autocorrelated red king crab recruitment models with multiple α and β parameters. Multiple parameters for a model configuration are shown vertically with the corresponding brood years. Crab type A indicates all males, and type L indicates legal males. Models consider 1960–1996 brood years ($n = 37$ observations).

		α		β		φ			
Crab type	Brood years	Est.	CV	Est.	CV	Est.	CV	RSS	AIC_c
L	1960–1996	0.49	0.52	6.3×10^{-5}	0.53	0.75	0.10	45.62	120.4
L	1960–1974	1.36	0.53	3.2×10^{-5}	0.35	0.66	0.13	41.85	119.0
	1975–1996	0.22	0.42						
L	1960–1974	0.48	0.39	3.8×10^{-5}	0.81	0.66	0.14	40.11	117.5
	1975–1996			2.8×10^{-4}	0.24				
L	1960–1974	0.78	0.58	5.8×10^{-5}	0.61	0.63	0.15	39.58	119.8
	1975–1996	0.35	0.46	2.4×10^{-4}	0.31				
L	1960–1974	0.83	0.48	6.0×10^{-5}	0.49	0.51	0.22	33.16	113.3
	1975–1984	0.05	0.43						
	1985–1996	0.55	0.38						
A	1960–1996	0.24	0.48	2.7×10^{-5}	0.70	0.73	0.11	43.74	118.0
A	1960–1974	0.70	0.53	4.7×10^{-5}	0.39	0.64	0.14	39.37	116.8
	1975–1996	0.13	0.39						
A	1960–1974	0.25	0.36	1.7×10^{-5}	0.93	0.63	0.15	39.70	117.1
	1975–1996			1.4×10^{-4}	0.30				
A	1960–1974	0.51	0.56	3.6×10^{-5}	0.54	0.59	0.17	38.40	118.7
	1975–1996	0.17	0.41	1.1×10^{-4}	0.43				
A	1960–1974	0.44	0.46	3.1×10^{-5}	0.52	0.44	0.28	29.57	109.0
	1975–1984	0.03	0.39						
	1985–1996	0.32	0.34						

Bay. Although our use of male crab abundance as a proxy for spawning abundance may be less robust than using female data, a lack of female abundance data until 1972, well after years of high stock abundance and strong recruitment, limits use of females in an S-R analysis for Kodiak red king crab. Nonetheless, autocorrelation is still suggested.

Among all autocorrelated Ricker configurations, estimated peak production of 2.0 to 3.4 million recruits resulted from 11.3 to 37.7 million male spawners. For our selected model with three α parameters, a total of 32.8 million male spawners provided an estimated 5.3, 0.4, and 3.8 million male recruits for the 1960 to 1974, 1975 to 1984, and 1985 to 1996 brood years, respectively. Because abundances of both spawners and recruits have been less than 1.0 million males since 1983, increased productivity for 1985 to 1997 relative to 1975 to 1985 seems contradictory with the failure of the population to rebuild after the commercial fishery closure since early 1982. Data uncertainty could be a factor in this seeming inconsistency, and several strong outliers were evident in the residuals patterns from the S-R models. For example, the 1997 recruit estimate of 5,000 male crab, accounting for approximately 25% of the residual sum of squares in the S-R models, is suspect and future analysis should explore the survey data from which this point is derived.

Another factor contributing to data uncertainty in the S-R relationship is the inability to accurately age red king crab, as well as assumed growth and maturity patterns (Powell 1967; McCaughran and Powell 1977; Bechtol and Kruse, in press). Changing environmental conditions probably alter growth rates and maturity schedules. For example, periods of slow (1980–1984, 1992–1993), medium (1985–1991), and fast (1972–1979) growth were associated with molting probability shifts for red king crab in Bristol Bay (Balsiger 1974; Zheng et al. 1995b). The Kodiak model assumption of a single S-R lag for the entire 45-year time series probably introduces process error into the analysis. Incorporating variable growth and maturity rates for Kodiak red king crab, although more realistic, would have introduced complexity and uncertainty into the S-R analysis because of the lack of annual data. To maintain a relatively simple S-R model, we assumed long-term population patterns to be represented by a single time lag between the year of parental stock reproduction and the year of recruitment. Based on the growth analysis of McCaughran and Powell (1977), our sensitivity analysis considered time lags ranging from 5 to 8 years between reproduction and recruitment. The optimal model is a lag-5 autocorrelated Ricker model based on all males and with three α parameters and one β parameter to accommodate different productivity periods (Tables 3, 4). Ultimately, a 5-year mean lag between reproduction and model recruitment implies a 6-year lag to legal size, shorter than the 7 to 8 years estimated by McCaughran and

Powell (1977), and perhaps suggesting a compensatory demographic mechanism of faster growth for what has become a depressed population.

The inconsistency between productivity and abundance may also indicate depensation in the Kodiak population. For example, crab abundance may be regulated at a low-density, stable equilibrium by predation, or a predator pit (May 1977; Peterman 1977; Liermann and Hilborn 2001). However, our analysis through a depensatory model, even when substituting depensation for only one or two of the periods in our optimal model, failed to confirm depensation. Liermann and Hilborn (2001) concluded that because demography and environmental variability make depensation very difficult to detect, a lack of evidence cannot be interpreted as evidence that depensation is rare or unimportant. In depensatory cases, future increases in the population may occur only under unusually favorable environmental conditions or declines in predation that result in increased recruitment.

Analysis of stock productivity should have sufficient contrast between years of high and low abundances to represent the range of potential productivity for a population (Hilborn and Walters 1992), but our analysis of S-R relationships for Kodiak red king crab was constrained in this regard by three issues. First, despite the availability of 45 years of abundance and recruitment data, values of stock abundance and recruitment for a large portion of the assessed years, those since the 1980s, were at low levels near the S-R curve origin (Figures 4A–D, 5B). These points near the origin represented over half of the data but introduced little contrast into the S-R relationship. Second, years of highest recruitment occurred in the early 1960s, corresponding to brood years in the late 1950s for which abundance estimates of the reproductive stock are unavailable (Table 2). Although previous research suggested that recruitment in the early 1960s was anomalously high (Rothschild et al. 1970; Burgner 1972; Bechtol and Kruse, in press), the strong recruitment levels observed from moderate spawning populations during that period, if under optimal environmental conditions, would fit well with the S-R relationships from our study. Third, the Kodiak stock was subject to high male harvest rates on a decreasing population abundance in the late 1970s, coupled with sex ratios increasingly skewed toward females (Orensanz et al. 1998; Bechtol and Kruse, in press). The resulting localized recruitment overfishing, coupled to recruitment failures in the mid-1980s, essentially created a "one-way trip," limiting data utility for stock dynamics modeling (Hilborn and Walters 1992).

In addition to the contradiction between relatively high productivity and low observed abundance, there are other indications of reduced resiliency in the population. Bechtol and Kruse (in press) noted increased variability in natural mortality after the regime shift in the mid-1970s. The magnitude of annual fluctuations in natural mortality again increased dramatically after 1988, complemented by a general increase in mean annual mortality. Such a pattern may indicate reduced resiliency due to low population size and a truncated age structure (Leaman and Beamish 1984; Kruse 1993; Berkeley et al. 2004). Kruse (1993) concluded that skip-molt males (those not molting in the current year) may predominate in mating success. Because males skip molt with increasing frequency as they grow beyond 125 mm CL (McCaughran and Powell 1977), our size of model recruitment, and larger males tend to have greater reproductive success (Paul and Paul 1997), reproductive contribution and skip-molting are both anticipated to increase with crab size. However, our lag-5 autocorrelated models showed slight improvement in AIC_c values if using an all-male versus legal-male currency with a single α and strong improvement with three α parameters (Table 4). Reproductive contribution by sublegal males arguably varies annually in response to environmental conditions that promote or suppress strong survival or faster growth, or both, and also large male availability, which depends on management strategies and corresponding fishing mortality. Our analysis, while characterizing long-term population trends using a single male currency, suggests that sublegal males have made important reproductive contributions to the Kodiak stock, perhaps at the expense of population resiliency. Finally, the reduction in red king crab abundance around Kodiak was accompanied by a severe range contraction. Dramatic geographic reductions from the 1970s to the 1980s were documented by the pot survey, which was conducted until 1986 (Johnson 1990). Fine-scale patterns in the red king crab spatial distribution cannot be derived from the more recent (1986–present) trawl survey data because of systematic survey bias, but verbal reports from local vessel operators continue to indicate a very limited spatial crab distribution. Thus, crabs are recruiting into a much smaller habitat area and are probably subject to intense competition or predation, including cannibalism. Although low population size and high interannual survey variability have substantially increased measurement error in the stock assessment (Bechtol and Kruse, in press), we postulate that low population abundances in recent years make the population particularly vulnerable to density-dependent factors, such as difficulty in finding mates during the mating season. These aspects reiterate the need to maintain a broad age-structure to provide resiliency in managed populations of long-lived species (Leaman and Beamish 1984; Kruse 1993; Berkeley et al. 2004).

Our optimal model indicated at least three periods of different productivity (Table 5); estimated transitions in 1975 and 1985 would have been expressed as recruitment in 1980 and 1990 by the lag-5 model. We did not conduct an exhaustive search of potential regime transition points, and future analysis should consider time-varying parameters through procedures such as a Kalman filter (Peterman et al. 2000). However, our transitions are consistent with the generally recognized climate regime shifts of 1976 and 1989 for the North Pacific (Anderson and Piatt 1999; Hare and Mantua 2000; Kruse 2007; Mueter et al. 2007), particularly given that response to ecological changes can vary temporally by species (Rodinov and Overland 2005). In particular, the climate regime shift in the North Pacific during the late 1970s was associated with aspects such as increased ocean temperatures and increased abundances of predatory fishes (e.g., Pacific cod *Gadus macrocephalus*). A study of the decline in the Kachemak Bay stock of northern shrimp *Pandalus borealis* found that a strong increasing trend in natural mortality followed the 1976 to 1977 regime shift, paralleling trends in increased Pacific cod abundance (Fu and Quinn 2000; Fu et al. 2000). That study found natural mortality to be the most important factor controlling this stock during the late 1970s and early 1990s. Red king crab instars are susceptible to predation by a variety of groundfish and shellfish (e.g., Jewett 1978; Jewett and Powell 1979) and to cannibalism (Broderson et al. 1990). We speculate that predation is a likely cause for increased natural mortality and reduced recruitment during the latter portion of the time series examined here. A cursory analysis of the Alaska Department of Fish and Game (ADFG) pot survey data revealed a strong increase in relative abundance of Pacific cod in nearshore waters around Kodiak at a time when the king crab population drastically declined (results not shown). However, predation on any life stage of red king crab and the corresponding impact on future recruitment have been poorly documented (Livingston 1989; Dew and McConnaughey 2005; Zheng and Kruse 2006).

Our study represents the first development of an S-R relationship for the red king crab population around Kodiak, Alaska. A density-dependent relationship is suggested by a dome-shaped relationship in the S-R data. Future analyses of Kodiak red king crab should examine temporal changes in stock and recruitment with respect to oceanographic conditions and ecological factors. In addition, the potential interaction between crab stocks and other fisheries, such as bottom trawl fisheries for groundfish and shrimp, merits further research because of potential impacts to the benthic crab habitats and direct but often undocumented crab mortality, particularly that of egg-bearing females (Armstrong et al. 1993; Dew and McConnaughey 2005). Moreover, the relationship between crab recruitment and environmental and ecological factors, such as temperature effects on match–mismatch of crab larvae and their prey, is of particular interest, especially given that larvae must feed within 2 to 6 d of hatching for optimal survival (Paul et al. 1989). We will explore these relationships more completely in a forthcoming article.

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