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ABSTRACT: We developed a method to estimate male reproductive potential and effective spawning biomass and used the results from a length-based model to develop a stock–recruitment relationship for Bristol Bay Tanner crab *Chionoecetes bairdi*. Weak and strong recruitment occurred with both low and high effective spawning biomass; however, recruits are not strongly associated with effective spawning biomass. Recruitment is highly autocorrelated. The strongest recruitment is almost 100 times as large as the weakest recruitment, and the largest effective spawning biomass is more than 10 times as large as the lowest. An autocorrelated Ricker curve is flatter and fits the observations better than an ordinary Ricker curve. Much of the recruitment variation can be explained by autocorrelation or cycle; thus, environmental factors are likely to play a very important role in recruitment success.

INTRODUCTION

A stock–recruitment (S–R) relationship describes a probable recruitment level of progeny from a given reproductive stock size. Such a relationship can be created by density-dependent predation, cannibalism, and food or space limitations. Inability or difficulty to find mates at low densities can also produce a strong relationship at low reproductive-stock levels. The commonly used S–R models are dome-shaped curves, developed by Ricker (1954), and asymptotic curves by Beverton and Holt (1957).

The S–R relationship has important implications for harvest strategies. If no such relationship exists — i.e., recruitment is not related to the corresponding reproductive stock size — then the optimal harvest strategy may be to harvest all crabs that have reached their maximum economic value. But many experiences around the world show that if stocks are heavily exploited, then recruitment will eventually be reduced. Because recruits are survivors from eggs that are spawned by the parent stock, it follows that depressed reproductive stocks will produce few eggs and few recruits in a closed population. Even if the S–R relationship has not been clearly demonstrated for each stock and species, it is prudent to assume an effect of stock size on recruitment, at least at low reproductive stock levels, to avoid risk of commercial extinction. Because of limited data, S–R relationships have not been estimated for the large majority of crab stocks in Alaska.

In this study we used results from a length-based model (LBA; Zheng et al. 1998) to develop an S–R relationship for Bristol Bay Tanner crab *Chionoecetes bairdi*. First, we developed a method to compute male reproductive potential based on a literature review of Tanner crab reproductive biology and data on size-at-maturity derived from summer trawl surveys conducted by the National Marine Fisheries Service (NMFS). Second, we estimated effective spawning biomass from mature female abundance and male reproductive potential. Finally, we fit effective spawning biomass and recruitment data to both an ordinary and an autocorrelated Ricker model and examined residual patterns from the fits. We also fit other reproductive biomass indices to S–R models for comparison.

Methods

Data

Time series of recruitment and abundance by sex, size, and shell condition from 1975 to 1997 were derived from the LBA (Zheng et al. 1998) updated with current “area-swept” estimates of abundance from trawl

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Table 1. Summary of "area-swept" survey female abundance (≥80 mm CW), total catch from all fleets and catch per unit effort from the Japanese fleet for eastern Bering Sea Tanner crab and estimated effective spawning biomass (1000 t) for Bristol Bay Tanner crab from 1968 to 1978. Catch and catch per unit effort are lagged 1 year. See text for the detailed methods to estimate effective spawning biomass.

Year	Survey Abundance ($\times10^6$)	Smoothed Abundance (A)	Effective Spa. Bio. (B)	Ratio (B/A)	Total Catch ($\times10^6$)	Catch Per Unit Effort			Ratio (B/D)
						Tangle Net	Pot	Combined (D)	
1968			40.26		22.98	34.02	12.13	12.82	3.140
1969			36.41		22.59	27.93	12.10	11.60	3.140
1970			36.86		18.10	29.09	11.93	11.74	3.140
1971			41.08		14.87		13.08	11.43	3.140
1972			29.09		9.57		9.27	11.61	3.140
1973	97.18	127.53	33.51	0.263	13.16		12.47	11.34	2.955
1974	189.15	148.36	38.99	0.263	9.42		12.28	11.73	3.324
1975	158.76	172.46	45.64	0.265	14.84		10.43		
1976	169.48	198.75	49.92	0.251	24.94				
1977	268.01	177.47	48.37	0.273	27.95				
1978	94.91		36.30		18.29				

surveys and commercial catch. Observed size-at-maturity and clutch condition data were collected from trawl surveys. Recruitment estimated by the LBA was assumed to index year-class strength. It is only an index because it is affected by survey gear catchability and because the LBA does not model crabs with carapace widths (CW) less than 70 mm for females and 93 mm for males. Also young crabs recruiting to the modeled stock in any given year probably consist of more than one age group because of variation in growth. However, as long as this recruitment index is predominated by one age group of crabs and reasonably measures relative strengths of year classes, the overall shape of the S–R curve will not be greatly affected.

Abundances before 1975 were not estimated by the LBA because electronic data files were not available. However, area-swept estimates of female crabs ≥80 mm CW from trawl surveys in 1973 and 1974 and catch per unit effort (CPUE) from the Japanese fleet for large male Tanner crabs from 1968 to 1976 are available for the eastern Bering Sea (Table 1). These data were used to estimate effective spawning biomass and other reproductive biomass indices from 1968 to 1974.

Time from Mating to Recruitment

Because of inadequate age information, the time from mating to recruitment has to be derived from growth and other observations. Female recruitment is distributed over 70–104 mm CW, but 97.0% is 70–94 mm CW and the mean is 80.4 mm CW. Male recruitment is distributed over 93–127 mm CW, 92.3% being 93–117 mm CW and the mean being 105.5 mm CW. On average, female and male Tanner crabs with 80.4-mm and 105.5-mm CWs in the northern Gulf of Alaska are 5 and 6 years old (since hatching); time lags since mating are 6 and 7 years (Donaldson et al. 1981). But juvenile Tanner crabs should grow faster in the northern Gulf of Alaska, where temperatures are higher, than in Bristol Bay (Brad Stevens, NMFS, Kodiak, personal communication). In addition, the strong cohort recruited to the model in 1987 (females) and 1988 (males) may be progeny of the 1980 reproductive stock hatched in 1981 because a large number of 30–35-mm-CW juvenile crabs, which we estimate to be 2 years old, were caught in the NMFS summer trawl survey in 1983. Therefore, we assumed the time from mating to recruitment is 7 years for females and 8 years for males. This is consistent with a recent modeling study of wind effects on Tanner crab larvae (Rosenkranz et al. 1998). Because male and female recruits have the same trend with 1-year difference in age, female recruitment in year *t*-1 was added to male recruitment in year *t*, and a time lag of 8 years was used for total recruitment. For example, females recruited in 1975 were assumed to be from the same cohort as males recruited in 1976. Time lags of 7 and 9 years were also examined for sensitivity of the S–R relationship to this parameter.

Size at Maturity

Male Tanner crab size at maturity depends on the definition of maturity. Males as small as 55–65 mm CW are physiologically mature and capable of providing sufficient sperm to fertilize an egg clutch under laboratory conditions (Adams and Paul 1983; Paul 1992). Although males <114 mm CW are capable of inseminating softshell primiparous females, they cannot mate with multiparous females (Paul and Paul 1996). In natural populations mating males can be much larger; off Kodiak Island mean size of males was 107 mm CW for mates of primiparous females and 131 mm CW for mates of multiparous females (Stevens et al. 1993). Mean CW of males is 33 mm larger than that of their partners (Stevens et al. 1993). Claw size also matters; few small-clawed males are observed in mating pairs (Stevens et al. 1993), so claw size is used as a proxy for maturity status. Relationships between chela height and CW for small- and large-clawed males are used to estimate size at which 50% of the males are functionally mature. Estimates of the 50% maturity are 100 mm CW (Stevens et al. 1993), 110 mm CW (Brown and Powell 1972), and 112 mm CW (Donaldson et al. 1981) for Kodiak male Tanner crabs, and 115 mm CW for eastern Bering Sea male Tanner crabs (Somerton 1980). For convenience, we modeled size-at-maturity for Bristol Bay male Tanner crabs ≥113 mm CW, the cutoff between two 5-mm-CW intervals.

Maturity status of female Tanner crabs can be determined directly by observations of egg clutches during trawl surveys. Proportions of mature crabs by 5-mm-CW intervals were fit to a logistic model by least squares methods to estimate sizes at 50% maturity. Sizes at 50% maturity for female Tanner crabs changed over time and were <80 mm CW for most years (Figure 1). The largest size at 50% maturity occurred in 1987 in association with strong recruitment, but maturity size was not closely related to recruitment strength (Figure 1). As expected, sizes at 50% maturity for newshell females were larger than those for oldshell females because all immature females are newshells.

To estimate effective spawning biomass, we assumed that female Tanner crabs mature at a minimum of 80 mm CW. Although sizes at 50% maturity were <80 mm CW during most of the years from 1975 to 1997, 80 mm CW was at the middle between the largest and smallest sizes at 50% maturity. Abundance

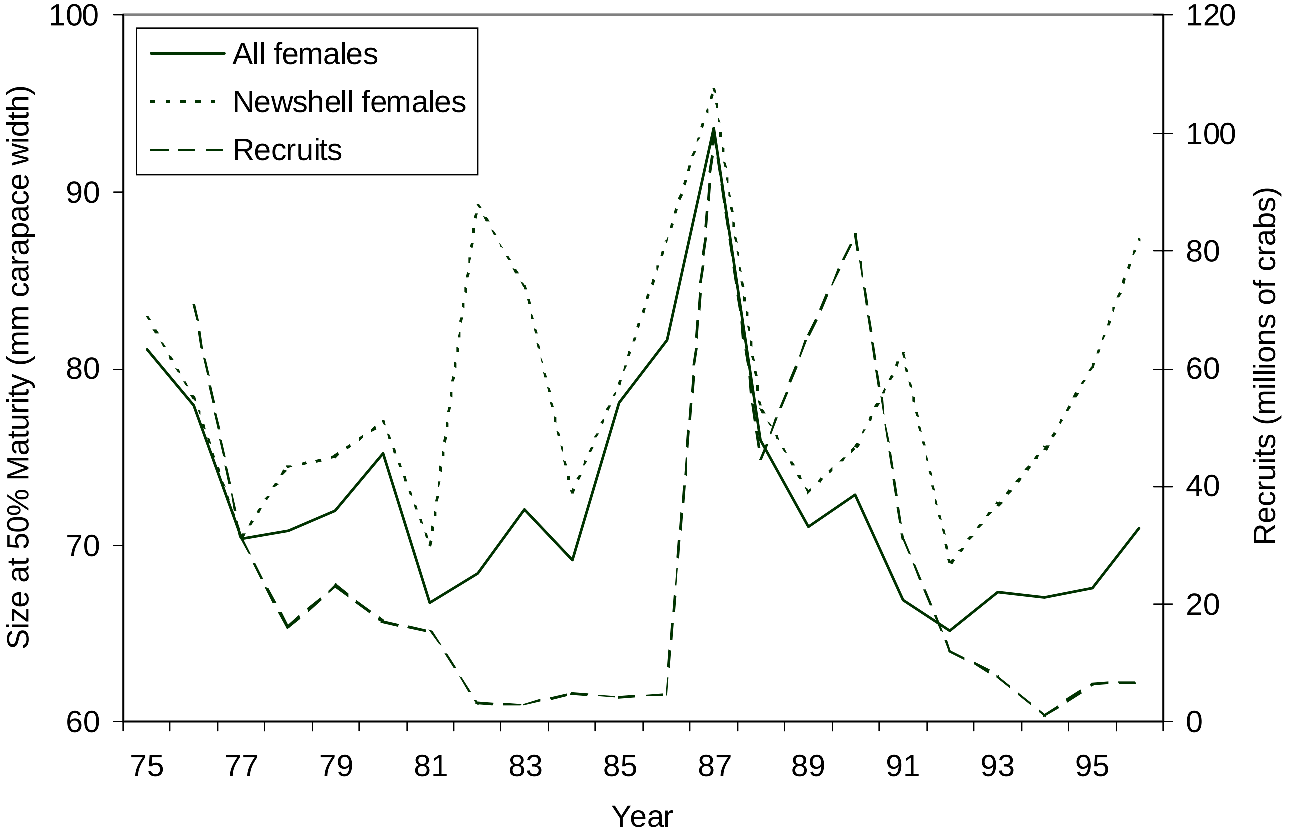


Figure 1. Size at 50% female maturity estimated from clutch data from NMFS surveys and recruitment estimated by a length-based analysis for female Bristol Bay Tanner crabs from 1975 to 1997.

estimates are less reliable for smaller crabs because it is difficult for trawls to catch small crabs. Although our assumed maturity size of 80 mm CW is much smaller than the 93 mm CW estimated by Somerton (1981), who used mean size of mature females, it more accurately represents observed sizes at 50% maturity during the 1975–1997 period we modeled. Use of mean size of mature females would be inappropriate as a minimum size for maturity and would greatly underestimate female mature abundances during most years.

Computation of Effective Spawning Biomass

The average number of females a male can mate each year depends on molting-period duration of the female population, duration of male attendance during mating, population density, and male fertilization capability. Molting season for primiparous females in Womens Bay, Kodiak Island, each year is 6 months, and aggregation and synchronous hatching of multiparous females may result in only 2–3 weeks of mating opportunity for an aggregation and 1–2 months for the whole population (Brad Stevens, NMFS, Kodiak, personal communication). Although non-aggregation matings of multiparous females were often observed in shallow water in Southeast Alaska, the mating season may also be 1–2 months (Bob Stone, NMFS, Juneau, personal communication). To produce viable clutches, primiparous females need to be mated within 27 d after molting and multiparous females need to be mated within 7 d after hatching of the previous year's clutch (Paul and Adams 1984). Precopulatory relationships between mating partners last 1–12 d (Donaldson and Adams 1989). A mature male can mate with a maximum of 8–10 females in a laboratory setting during a breeding season (Paul 1984). Because of discrete spatial distributions and a limited mating window, we hypothesize that a higher density of females results in a larger average number of females mated per male during a breeding season. Based on these considerations, we assumed that a male could mate, on average, with a maximum of 5 primiparous females and 3 multiparous females at high population densities and with 1 primiparous and 1 multiparous female at low densities. Therefore, a male can mate with up to 8 females under ideal conditions and 2 females under the worst case. The maximum average number of females per male at a density between low and high was linearly interpolated. The high density was assumed to be the highest estimated density or higher during 1975–1997, and the low density to be the lowest estimated density or lower during the same period. We examined different combinations of mate numbers to see which combinations would have resulted in inadequate numbers of males for mating in the historical data set. Because female crabs molt at least once per year before maturity, we assumed that newshell mature females are primiparous and oldshell mature females are multiparous.

Somerton (1981) speculated, based on anecdotal information, that bipartite breeding occurs for Tanner crabs. In bipartite breeding, pubescent and multiparous females are separated by distance and depth and mated by different sizes of males. Stevens et al. (1993) observed this phenomenon in Kodiak Tanner crabs. Although Stevens et al. (1993) observed that sizes of males mating with pubescent females were ≤125 mm CW during the April and May overlap breeding season of multiparous females, it is possible that larger males mate with pubescent females, especially during a pubescent-only breeding season (January–March). So, we assumed males <138 mm CW can mate with both pubescent/primiparous and multiparous females, but males >137 mm mate with only multiparous females. This assumption will slightly affect mating schedule only in years such as 1987 when an extremely strong recruitment with relatively large sizes at maturity followed several years of poor recruitment.

Shell conditions also affect mating; recently molted males do not mate for at least 99 d after molting, and oldshell males dominate matings contested by newshell males (Paul et al. 1995). Stevens et al. (1993) reported that the proportion of oldshell males grasping multiparous females was much higher than proportions with pubescent partners. The proportion of oldshell males caught by trawls was even lower. Based on this information and the molting duration for primiparous females, we assumed that only 30% of newshell males participate in mating with pubescent or primiparous females and 10% with multiparous females. For convenience, these mature males participating in mating are termed as "matable" males.

Female Tanner crabs can store sperm for more than 1 year. Stored sperm from the first mating cannot fertilize the second year's clutch (Paul and Paul 1992); however, stored sperm from multiple matings may fertilize the 2 subsequent years' clutches (Paul 1984). Therefore, for multiparous females, reduction of effective spawning biomass occurs only when lack of male partners occurs for 2 consecutive years.

Annual effective spawning biomass, S_t, was estimated as

$$S_t = \sum_l \left[\left(NF_{l,t}\, nr_t + OF_{l,t}\, or_t\right) W_l\right], \quad l \geq 80 \text{ mm CW}, \qquad (1)$$

where $NF_{l,t}$ and $OF_{l,t}$ are newshell and oldshell female abundances in width class l and year t, W_l is mean weight of female crabs in width class l, i is the mid-width of width class l, and nr_t and or_t are the ratios of male reproductive potentials TNM_t and TOM_t to newshell and oldshell mature female abundances TNF_t and TOF_t (≥80 mm CW) in year t, respectively; that is,

$$nr_t = TNM_t \,/\, TNF_t;\; or_t = \max\left[TOM_{t-1} \,/\, TOF_{t-1},\; TOM_t \,/\, TOF_t\right]. \quad (2)$$

If nr_t or or_t is >1, we set them equal to 1. The male reproductive potentials for newshell and oldshell mature females were defined as

$$\begin{aligned} TNM_t &= \sum_l \left[\left(0.3NM_{l,t} + OM_{l,t}\right) nn_t\right],\ 113\text{ mm} \le l \le 137\text{ mm CW}, \\ TOM_t &= \sum \left[\left(0.1NM_{l,t} + OM_{l,t}\right) on_t\right],\ l \ge 113\text{ mm CW}, \end{aligned} \quad (3)$$

where $NM_{l,t}$ and $OM_{l,t}$ are mature male crab abundances in width class l and year t with newshell and oldshell conditions, respectively, and nn_t and on_t are the maximum average number of newshell and oldshell females mated by a matable male in year t. We assumed nn_t and on_t as

$$\begin{aligned} nn_t &= i + j\left(TNF_t - a1\right) / \left(a2 - a1\right) \text{ and } i \le nn_t \le i + j, \\ on_t &= i + j\left(TOF_t - b1\right) / \left(b2 - b1\right) \text{ and } i \le on_t \le i + j, \end{aligned} \quad (4)$$

where $a1$ and $a2$ are the lowest and highest estimated mature newshell female abundances from 1975 to 1997 (1.2 and 78.5 millions crabs), $b1$ and $b2$ are the lowest and highest estimated oldshell mature female abundance during the same period (5.7 and 60.8 millions of crabs), and i and $i+j$ are the maximum average mates per matable male at the low and high female abundances. As stated above, i was assumed to be 1 for both newshell and oldshell females, and j was assumed to be 4 for newshell females and 2 for oldshell females. Note that equation (4) is consistent with our assumption that a matable male can mate with 1 primiparous (newshell) and 1 multiparous (oldshell) female at low population densities and 5 primiparous and 3 multiparous females at high densities.

We used area-swept estimates of female crabs ≥80 mm CW from trawl surveys in 1973 and 1974 and CPUE from the Japanese fleet from 1968 to 1976 to estimate effective spawning biomass from 1968 to 1974. A 3-point moving average was used to smooth area-swept estimates of female crabs from 1973 to 1977 and pot CPUEs from 1968 to 1975. In 1973 the smoothed female abundance consisted of 67% of the survey abundance in 1973 and 33% of the survey abundance in 1974. Average of ratios of estimated annual effective spawning biomasses to smoothed female abundances in 1975–1977 was used to convert smoothed female abundances in 1973 and 1974 into effective spawning biomasses. During 1968–1972, female data were lacking, so male data were used as proxies. Average of ratios of estimated effective spawning biomasses in 1973 and 1974 to smoothed pot CPUEs in 1974 and 1975 were used to convert CPUEs from 1969 to 1973 into effective spawning biomasses from 1968 to 1972. Because the commercial catch consisted of primarily large males, we assumed the CPUE in year t represents the female abundance in year t-1. Because both pot and tangle net CPUEs are available during 1969–1971, 2 CPUEs were averaged each year; for comparison to the pot CPUEs in 1972–1974, the sum of averaged CPUEs was adjusted to equal the sum of pot CPUEs in the same period.

Stock–Recruitment Models

Annual recruitment is described by an autocorrelated Ricker S–R model,

$$R_t = S_{t-k}\, e^{\alpha - \beta S_{t-k} + \upsilon_t}\ , \quad (5)$$

where k is recruitment age, α and β are constants, and $\upsilon_t = \delta_t + \varphi\, \upsilon_{t-1}$ as environmental noise. $\{\delta_t\}$ was assumed as a $N(0,\sigma)$. Equation (5) was linearized as

$$\text{In}\left(R_t \,/\, S_{t-k}\right) = \alpha - \beta\, S_{t-k} + \upsilon_t\ . \quad (6)$$

An autocorrelation regression procedure, AUTOGRE (SAS Institute Inc. 1988) with a maximum likelihood method, was used to estimate parameters α, β and φ for equation (6). Alternatively, we set $\upsilon_t = A \sin(2\pi t/P) + \delta_t$ and used a least squares approach to estimate parameters A and P, α and β being fixed at values estimated by the autocorrelation regression. When φ is equal to 0, equation (4) becomes an ordinary Ricker model.

Depensation could occur when reproductive biomass is extremely small. As an alternative S–R model, we assumed recruits as an exponential function of effective spawning biomass when effective spawning biomass is very small:

$$R_t = \kappa\, S_{t-k}^{\theta}\ . \quad (7)$$

Table 2. Proportions of biomass from females ≥80 mm CW as effective spawning biomass under different combinations of average mates per matable male (*i* and *i*+*j*, the maximum average mates per matable male at the low and high female abundances, respectively; see equation 4). The columns in bold are baseline assumptions.

	Mature Newshell Females								Mature Oldshell Females					
Year	$i = 1$ $j = 2$	$i = 2$ $j = 1$	$i = 1$ $j = 3$	$i = 2$ $j = 2$	**$i = 1$** **$j = 4$**	$i = 2$ $j = 3$	$i = 1$ $j = 5$	$i = 2$ $j = 4$	$i = 1$ $j = 1$	$i = 2$ $j = 0$	**$i = 1$** **$j = 2$**	$i = 2$ $j = 1$	$i = 1$ $j = 3$	$i = 2$ $j = 2$
1975	0.89	0.89	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1976	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1977	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1978	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1979	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.94	1.00	**1.00**	1.00	1.00	1.00
1980	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.91	1.00	**1.00**	1.00	1.00	1.00
1981	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.77	1.00	**1.00**	1.00	1.00	1.00
1982	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.76	1.00	**1.00**	1.00	1.00	1.00
1983	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.69	1.00	**0.87**	1.00	1.00	1.00
1984	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.83	1.00	**0.93**	1.00	1.00	1.00
1985	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.83	1.00	**0.93**	1.00	1.00	1.00
1986	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.84	1.00	**0.85**	1.00	0.87	1.00
1987	0.31	0.36	0.40	0.45	**0.49**	0.54	0.57	0.80	1.00	1.00	**1.00**	1.00	1.00	1.00
1988	0.60	0.61	0.79	0.80	**0.99**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1989	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	0.96	1.00	**1.00**	1.00	1.00	1.00
1990	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1991	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1992	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1993	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1994	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1995	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1996	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00
1997	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00	1.00	1.00	**1.00**	1.00	1.00	1.00

Parameters κ and θ were estimated with a least squares approach using effective spawning biomass from 0 and 3 smallest estimated values. Estimated year classes associated with effective spawning biomass within this range were below the autocorrelated Ricker curve.

As a comparison to effective spawning biomass, we also fit 2 other reproductive biomass indices to the autocorrelated Ricker S–R model. These 2 indices are mature female biomass (sum of female biomasses by CW times the corresponding observed maturity rates from females ≥70mm CW) and female biomass ≥80 mm CW. The same procedure for estimating effective spawning biomass from 1968 to 1974 was used to estimate mature female biomass during the same period. Female biomass ≥80 mm CW was equal to effective spawning biomass from 1968 to 1974.

Results and Discussion

Under our assumption that a matable male can mate with 2–8 mature females ($i = 1$ and $j = 4$ for newshell females and $j = 2$ for oldshell females), males are rarely limiting female fertilization (Table 2). Shortages were predicted from 1983 to 1988, but only the 1987 shortage of males was significant. Under likely alternative combinations of average mates per matable male, male reproductive potential generally exceeded the actual number of mature female crabs from 1975 to 1997. Lack of males for newshell females occurred only in 1987 for all combinations and 1975 and 1988 for some combinations of low and average mates per male. The exceptionally strong recruitment and extremely low population abundance of large crabs in 1987 caused exceptionally high estimated female size at 50% maturity for 1987 (93.6 mm CW; Figure 1); consequently, the mature abundance with the 80-mm-CW minimum size for maturity was overestimated and included many immature crabs. The <1.0 ratio of male reproductive potential to mature female abundance provides a way to reduce the overestimated mature biomass in 1987. Because of relatively long annual mating seasons for newshell females, lack of males for mating should not occur unless mature females greatly outnumber mature males.

Annual mating seasons for oldshell females are much shorter than for newshell females, and the aggregative mating behavior and a short mating window further make multiparous females more prone to mating failure due to lack of males than primiparous females. Fortunately, capability to store sperm for more than 1 year provides some protection against mating failure (Paul and Paul 1992). Male reproductive potential was less than oldshell mature female abundances from 1979 to 1986 and in 1989 under a scenario of low average mates per male (1 for low abundance and 2 for high abundance) and from 1983 to 1986 under our assumed scenario of average mates per male (Table 2). Lack of mates for oldshell females seldom occurred with other combinations of high average mates per male (Table 2).

To include all recruitment data in the study of S–R relationships, we estimated effective spawning biomass from 1968 to 1974 based on trawl survey abundances and CPUE from the Japanese fleet. The CPUE and total catches from 1968 to 1974 indicate that crab abundances during this period were above the average from 1975 to 1997 but lower than abundances during the mid 1970s (Table 1). Estimated effective spawning biomass basically reflects this pattern. Limited trawl data in 1969, 1970, and 1972 are also available, but they are not necessarily comparable with the survey data since 1973. The survey catchabilities in 1970 and 1972 were smaller than later years; the commercial catch in 1972 was greater than the abundance of male crabs ≥130 mm CW estimated from the trawl survey. Zheng et al. (1995) estimated the survey catchability for mature female red king crab *Paralithodes camtschaticus* in Bristol Bay to be 0.25 in 1972. Estimated effective spawning biomass from the trawl survey in 1972 will be similar to our current estimate and about 10% lower than that in 1973, if this catchability is applied to the 1972 data.

Recruits are not strongly associated with effective spawning biomass; both weak and strong recruitment occurred with both low and high effective spawning biomass (Figure 2). The strongest recruitment is almost 100 times as large as the weakest recruitment, and the largest effective spawning biomass is more than 10 times as large as the lowest one (Figure 2). Variation of recruitment caused great fluctuation of population abundance over time. Strong year classes occurred in the late 1960s and early 1980s, and weak year classes occurred in the mid and late 1970s and mid and late 1980s; thus, recruitment was highly autocorrelated. As expected, the autocorrelated Ricker curve ($\alpha = 2.0402$, $\beta = 0.0563$, $\varphi = 0.73$, $r^2 = 0.72$, df = 19) is flatter and a better fit than the ordinary Ricker curve ($\alpha = 2.3543$, $\beta = 0.0700$, $r^2 = 0.44$, df = 20; Figure 2). Residuals from the ordinary Ricker curve were still highly autocorrelated. The Ricker curve with cyclic residuals (α=2.0402, β=0.0563, A=1.2676, and P=12.9464) fit the observations as well as the autocorrelated Ricker curve (Figure 3). The exponential S–R was fit with effective spawning biomass of 6395 t or less (Figure 3), and the results ($\kappa = 0.2031$, $\theta = 2.8031$; effective spawning biomass in 1000 t) are highly uncertain because only 3 pairs of data are available.

Much variation of recruitment can be explained by autocorrelation or cycle; thus, environmental factors are likely to play a very important role in recruitment success. Some environmental conditions may trigger a switch between weak and strong recruitment from period to period. Rosenkranz et al. (1998) suggested that winds from the northeast are favorable to larval retention and recruitment, but the patterns of winds from the northeast are not consistent with periods of weak and strong recruitment all the time. Alternative explanations include groundfish predation and competition and the possibility that the stock affects recruitment differently than we modeled. Spawning geography, i.e., the spatial distribution of spawners, is one possible confounding effect of stock on S–R relationships.

Strong autocorrelation of recruitment time series and periodic or quasiperiodic behavior of recruitment are common in many crab stocks and some fish stocks. For Bristol Bay red king crab strong recruitment occurred in the mid and late 1970s, and weak year classes occurred in the late 1980s and early and mid 1990s (Zheng et al. 1995). Recruitment is autocorrelated for other crab stocks in Alaska as well (Zheng and Kruse *in press*). Recruitment to red king crab stocks in the northern Gulf of Alaska and along the Aleutian Islands was strong during the late 1970s and has been weak since the mid 1980s. Recruitment to eastern Bering Sea blue king crab *Paralithodes platypus* stocks was strong in the mid and late 1970s, weak in the mid 1980s, and relatively strong in the 1990s. Recruitment to Tanner crab stocks in the northern Gulf of Alaska was strong in the mid 1970s and has been weak since the early 1990s. Snow crab *Chionoecetes opilio* in the northeast Gulf of Saint Lawrence alternates between series of strong and weak recruitment about every 8 years (Sainte-Marie et al. 1996). Recruitment of many fish stocks has periodicities ranging from 10 to 26 years (Koslow 1989). Although year classes for Bristol Bay Tanner crab from 1968 to 1989 showed a strong cyclic behavior, periods of 13 or 14 years (Figure 2), catch data (Otto 1990) indicate that the cycle was weaker or shorter for year classes from late 1950s to late 1960s

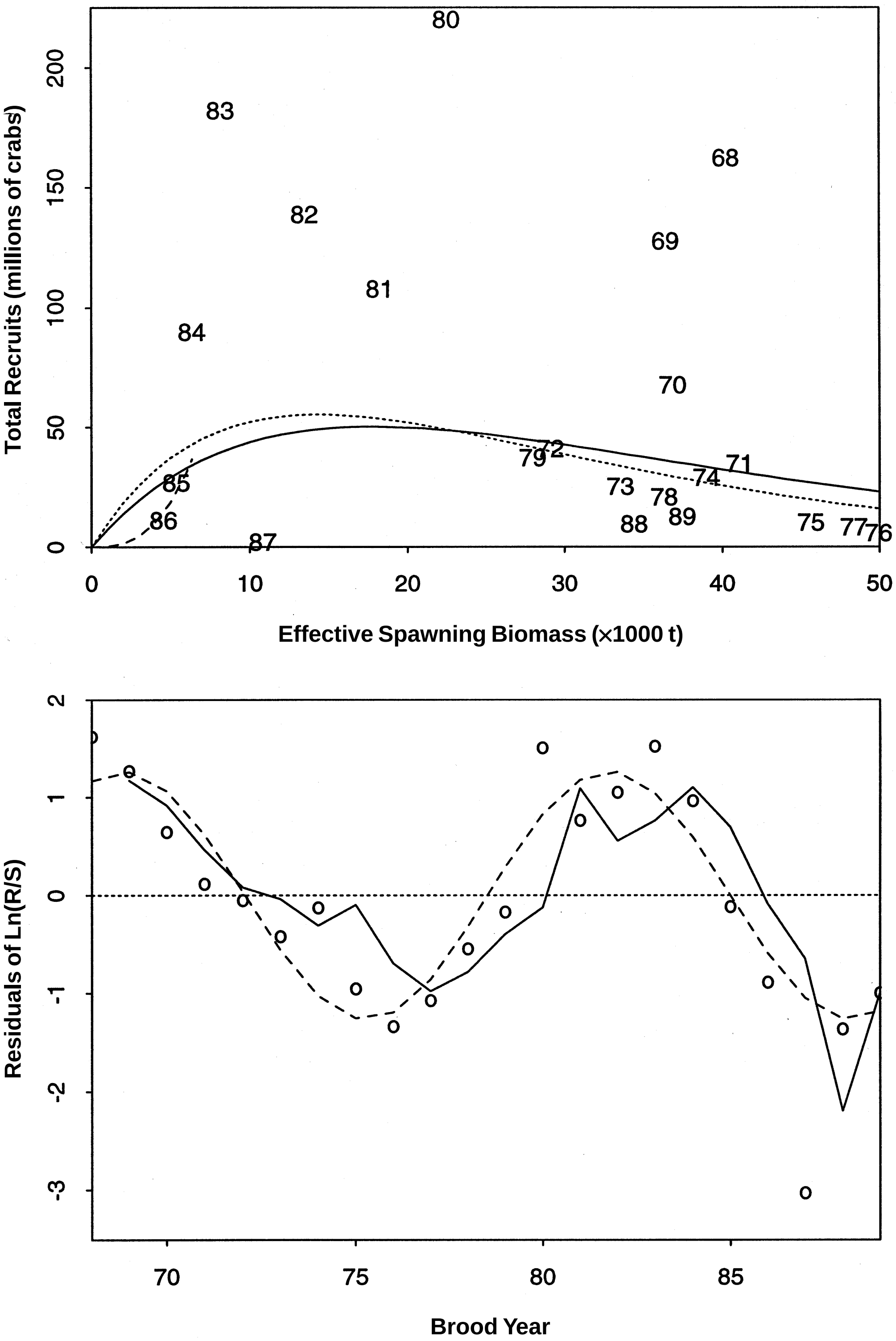


Figure 2. Relationships between effective spawning biomass and total recruits at age 7 (i.e., 8-year time lag; upper plot) and residuals of logarithm of recruits per effective spawning biomass from an autocorrelated Ricker curve (i.e., υ_t in equation 5; lower plot) for Bristol Bay Tanner crab. In the upper plot, numerical labels are brood year (year of mating), the solid line is an autocorrelated Ricker curve without υ_t values, the dotted line is an ordinary Ricker curve, and the dashed line is an exponential S–R curve. In the lower plot, the solid line represents autocorrelation and the dashed line is a sine function; both were estimated from residuals.

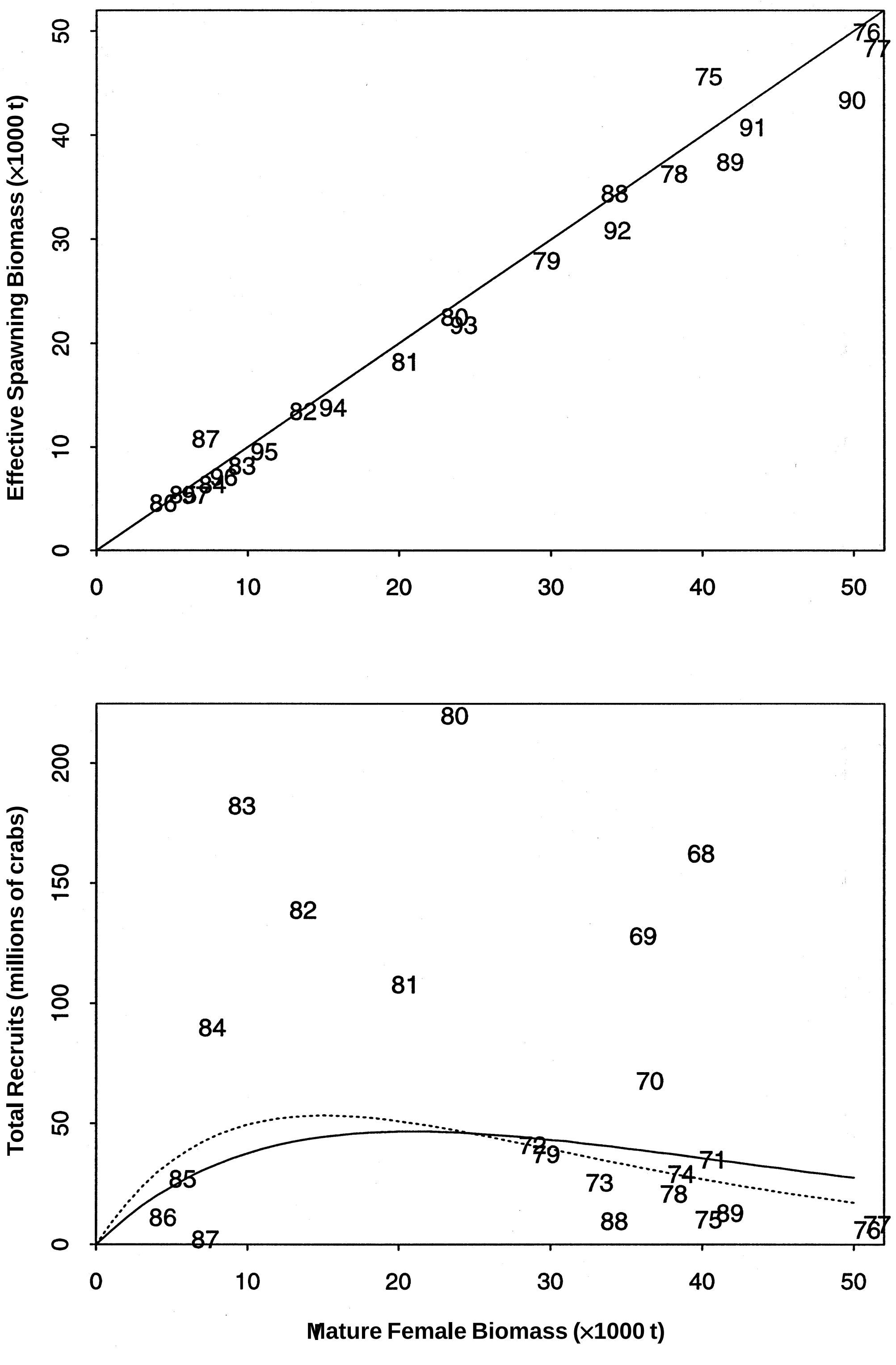


Figure 3. Effective spawning biomass versus mature female biomass from 1975 to 1997 (upper plot) and relationships between mature female biomass and total recruits at age 7 (i.e., 8-year time lag, upper plot) for Bristol Bay Tanner crab. Mature female biomass was computed from female abundances by CW times corresponding observed maturity rates from females ≥70 mm CW. In the lower plot, numerical labels are brood year, the solid line is an autocorrelated Ricker curve for total recruitment on mature female biomass without υ_t values, and the dotted line is an ordinary Ricker curve.

than from 1968 to 1989. Because of the brevity of available time series, the period length and even the existence of repeatable cycles are not well established. The strong recruitment cycles may also be caused in part by age class overlap in recruitment estimated by a size-based model. Nevertheless, despite uncertainty about the details, recruitment of Bristol Bay Tanner crab appears to be at least quasiperiodic.

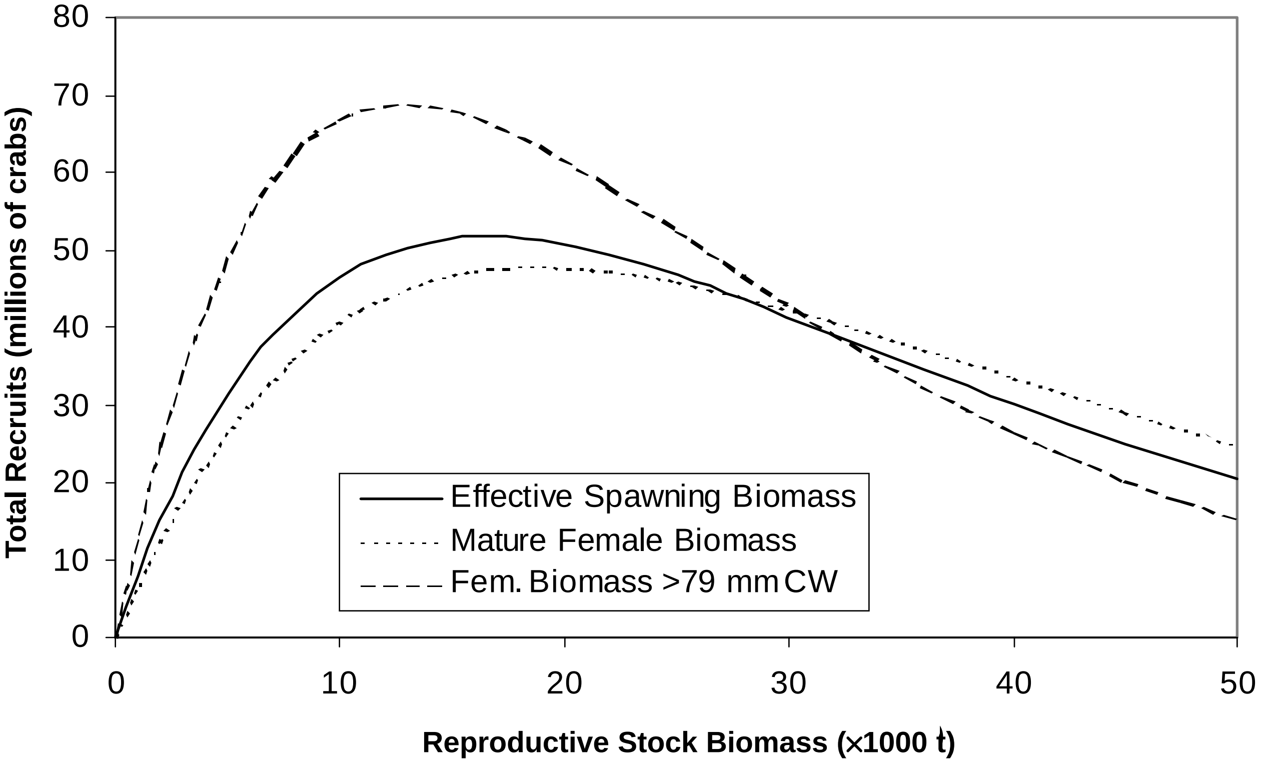
Estimates of effective spawning biomass were slightly lower than estimates of mature female biomass for most years from 1975 to 1997 (Figure 3). This is caused by 2 factors: (1) sizes at 50% maturity being lower than our assumed 80-mm CW for most years, and (2) inadequate males for mating in some years, based on our assumed number of mates per male. Inadequate males resulted in only a small reduction of effective spawning biomass in 5 years, except 1987. Interestingly, a 49% reduction in effective spawning biomass was still much higher than mature female biomass in 1987 (Figure 3). This is because the size at 50% maturity in 1987 was much larger than our assumed 80-mm CW, such that many immature crabs were included in computing effective spawning biomass. Our approach to estimating effective spawning biomass correctly reduces effective spawning biomass in an extreme situation like 1987, but our reduction is still not enough. Most of the differences between effective spawning biomass and mature female biomass are due to annual departures of the assumed 80-mm CW as the size at 50% maturity. Overall, our assumed 80-mm CW for female maturity closely separates mature from immature crabs during a large majority of years. If, similar to the estimate by Somerton (1981), a 90-mm or 95-mm minimum CW were used, we would greatly underestimate mature female biomass. Note that mature female biomass shown in Figure 3 does not include mature females <70 mm CW because the LBA does not model those crabs. A very small proportion of females <70 mm CW reach maturity.

Estimates of autocorrelated Ricker S–R curves with 3 reproductive biomass indices are illustrated in Figure 4. The curve with mature female biomass ($r^2 = 0.73$ and df = 19) was similar to the curve with effective spawning biomass (Figures 3, 4). But the curve estimated with female biomass ≥80 mm CW ($r^2 = 0.73$ and df = 19) was much more dome-shaped than the other 2 curves (Figure 4). The strong dome-shaped curve appears to be an artifact caused by the overestimated reproductive biomass index in 1987 by female biomass ≥80 mm CW. The estimated curve appears to be very sensitive to the 1987 data point that had an extremely low recruitment. The residuals from the 3 curves had similar cyclic features (Figure 4).

Because estimated S–R curves with mature female biomass and effective spawning biomass were similar, why should we not discard effective spawning biomass and just use mature female biomass for simplicity? The answer lies with the reasons why the curves were similar and how the S–R curve will be used. The 2 curves were similar because lack of males for mating rarely occurred in the time series of available data. If mature males are a limiting factor on reproductive success in the future, then the 2 curves may be different. The S–R relationship estimated with mature female biomass assumes that mature males are not a limiting factor on reproductive success, but we are not convinced that males could not become limiting under female-predominated sex ratios at low stock sizes. The advantage of effective spawning biomass is that it incorporates mature male abundance into a reproductive biomass index based on our current understanding of Tanner crab reproductive biology. In addition, the S–R relationship estimated with effective spawning biomass can be used in computer simulations to evaluate alternative harvest strategies as well as to explore the effects of mature males on reproductive success.

Sensitivity of estimates of effective spawning biomass from 1968 to 1974 on estimates of S–R relationships are illustrated in Figure 5. Decreasing effective spawning biomasses from 1968 to 1974 by 19% had very little influence on the estimated S–R relationships, whereas increasing the effective spawning biomasses by 22% would shift the peak of the dome of the S–R curve to correspond with a larger effective spawning biomass. The impact of increasing effective spawning biomasses was larger than the decrease because such an increase moved the high recruitment into an area associated with the maximum observed effective spawning biomass. Based on catch, CPUE, and limited survey data, it is very unlikely that effective spawning biomasses from 1968 to 1974 could reach the maximum observed level. Interestingly, the shapes of the S–R curves with or without data were almost identical for 1968–1972, when no survey data were used to estimate effective spawning biomass. Average year class size from 1973 to 1989 was lower than that from 1968 to 1989; therefore, recruitment levels were lower when data from 1968 to 1972 were not used. Without data from 1968 to 1973, recruitment levels were underestimated because there was 1 upward cycle and 1.5 downward cycles of recruitment. The residuals from the 4 curves had similar cyclic features.

The time lag from mating to recruitment is an important factor of the S–R curve. Although our best estimate of time lag is 8 years, a 7-year or 9-year time lag is also possible. The time lag may vary over time



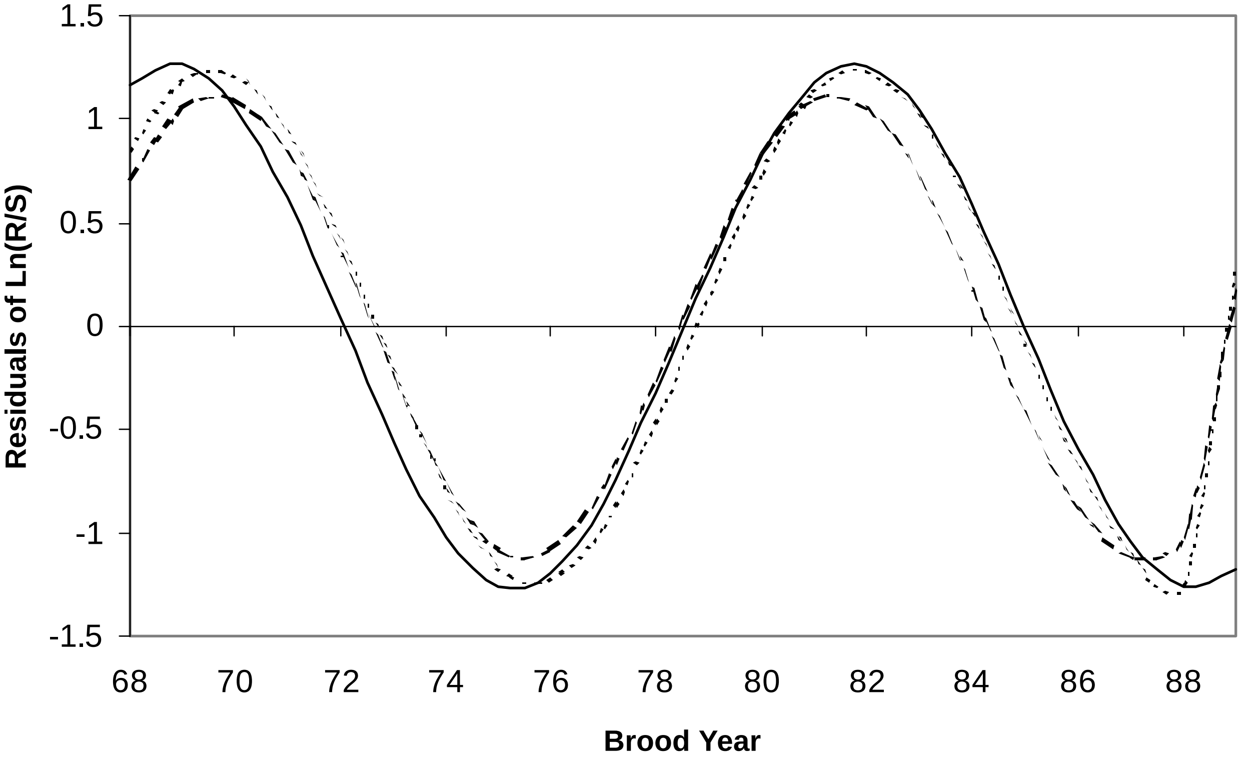


Figure 4. Relationships between 3 different reproductive biomass indices and total recruits at age 7 (upper plot) and residuals of logarithm of recruits per effective spawning biomass from an autocorrelated Ricker curve (i.e., υ_t in equation 5; lower plot) for Bristol Bay Tanner crab.

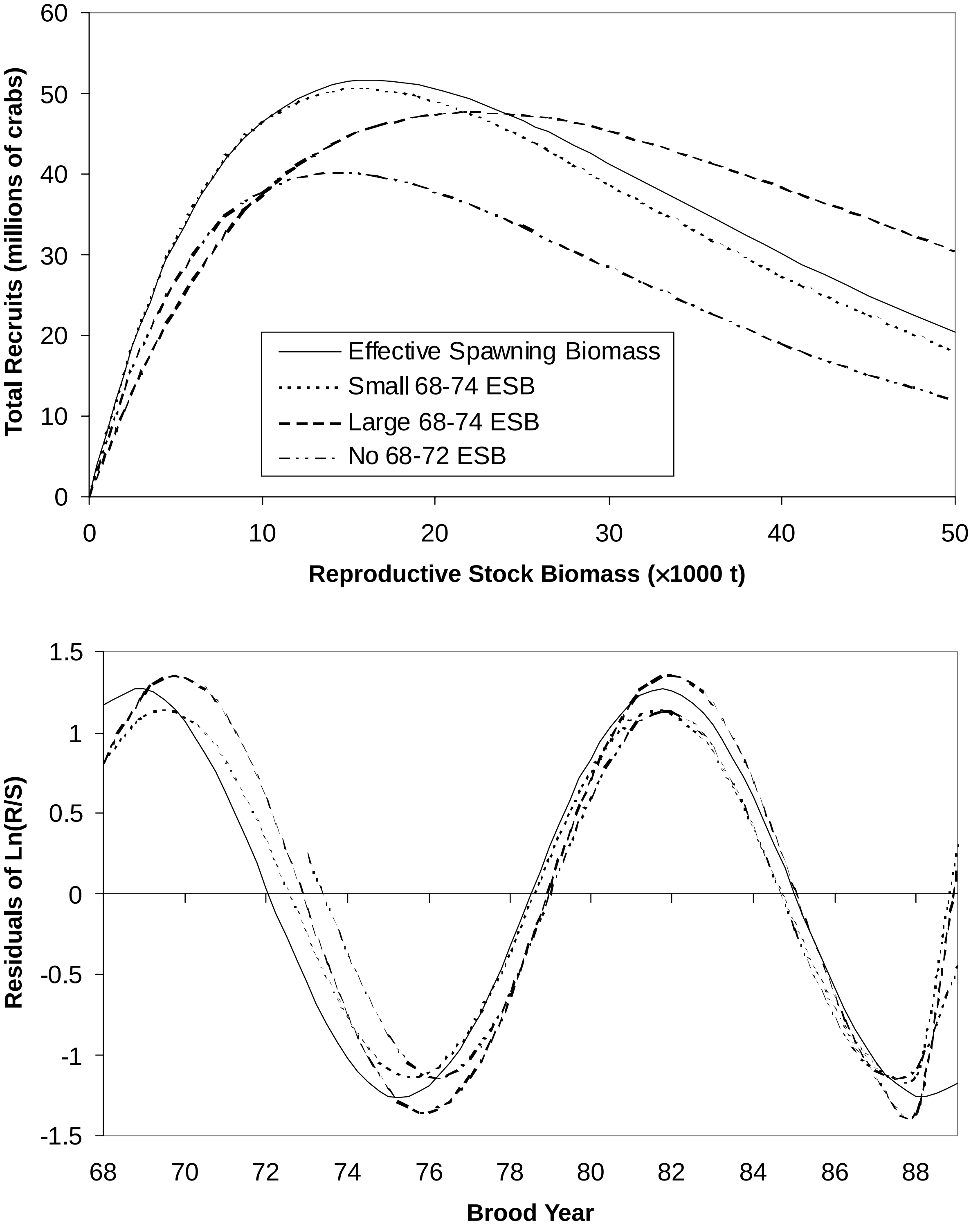


Figure 5. Relationships between effective spawning biomass (ESB) and total recruits at age 7 (upper plot) and residuals of logarithm of recruits per effective spawning biomass from an autocorrelated Ricker curve (i.e., υ_t in equation 5; lower plot) for Bristol Bay Tanner crab. "Small 68-74 ESB" represents a scenario that ESBs from 1968 to 1974 were reduced by multiplying the ratio (0.81) of mean ESB from 1975 to 1997 by the minimum ESB from 1968 to 1974; "large 68-74 ESB" represents a scenario that ESBs from 1968 to 1974 were increased by multiplying the ratio (1.22) of the maximum ESB from 1975 to 1997 to the maximum ESB from 1968 to 1974.

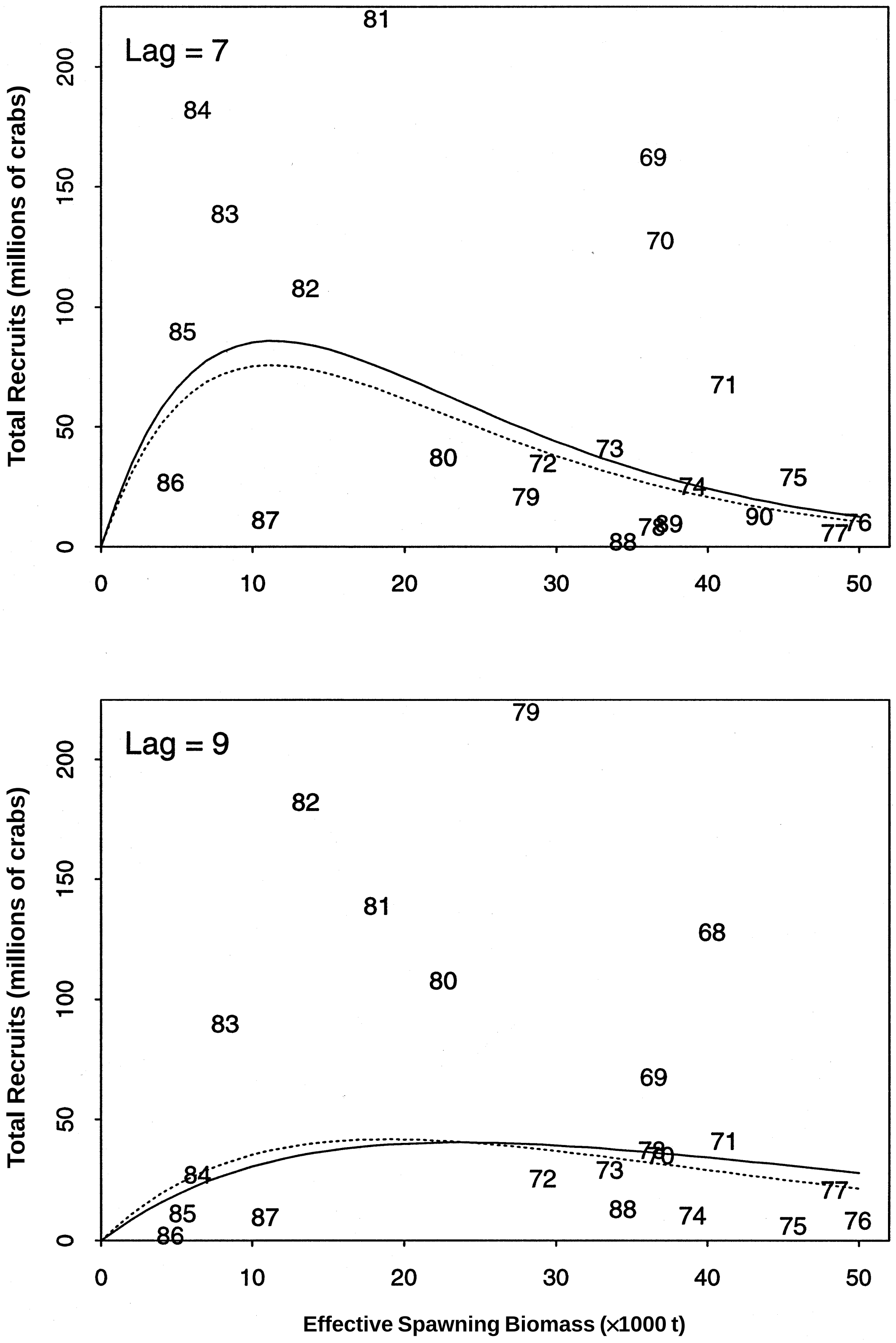


Figure 6. Relationships between effective spawning biomass and total recruits with 2 different time lags (in years) for Bristol Bay Tanner crab. Numerical labels are brood year, solid lines are autocorrelated Ricker curves without υ_t values, and dotted lines are ordinary Ricker curves.

as with red king crabs (Stevens 1990). Estimated S–R relationships are sensitive to the time lag. For a constant 7-year time lag, strong year classes in the early 1980s were associated with low effective spawning biomass, and the weakest year class, 1987, was related to relatively high effective spawning biomass; this resulted in a more domed-shape S–R curve and a better fit for the autocorrelated Ricker curve ($r^2 = 0.79$, df = 19; Figure 6) than for a constant 8-year time lag. The good fit for the 7-year time lag is partially caused by its coincidence with the half-cyclic period of 13–14 years of recruitment and effective spawning biomass. For a constant 9-year time lag, strong year classes occurred with a broad range of effective spawning biomass and weak year classes were associated with low and high effective spawning biomass; this resulted in a flatter S–R curve and a slightly poorer fit for the autocorrelated Ricker curve ($r^2 = 0.70$, df = 18, Figure 6) than for a constant 8-year time lag.

S–R relationships for crab stocks are difficult to develop because crabs lack retainable hard body parts, like scales, to age them. Without accurate ages, it is difficult to assign crab of varied sizes to particular year classes and match recruitment pulses to their corresponding reproductive stock. Temperature-dependent growth of juvenile crabs (Stevens 1990) introduces additional difficulty in estimating time from mating to recruitment. Lack of sufficient knowledge about complex crab reproductive biology also complicates estimating effective spawning biomass. However, because the autocorrelated Ricker S–R curve (Figure 2) is relatively flat and as long as estimated effective spawning biomass does not grossly depart from the true values, neither will affect the estimated S–R curve greatly.

Our study is the first attempt to estimate S–R relationships for a Tanner crab stock. A strong density-dependent relationship did not emerge after accounting for mates per male, effects of shell condition and size, and sperm retention by females. Our assumptions for time from mating to recruitment, minimum size for maturity, average numbers of mates per male, lack of mating by some newshell males, and exclusion of very large males for mating with newshell females are based on our current understanding of Tanner crab growth and reproductive biology. We recommend new studies on spawning geography, the proportions of oldshell and newshell males that participate in spawning migrations, and effects of senescence on male and female reproductive capability. Additional studies on environmental effects on growth and recruitment would also be valuable. As our understanding of Tanner crab biology increases in the future, we will be able to refine these S–R relationships.

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