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# Podding Behavior of Adult King Crab and Its Effect on Abundance-Estimate Precision

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## Abstract

The Alaska red king crab, *Paralithodes camtschaticus*, is a major target of the Bristol Bay stock assessment bottom-trawl survey conducted annually by the U.S. National Marine Fisheries Service. Because of the difficulty of sampling extremely patchy spatial distributions, it is important to know whether the podding behavior documented for juvenile red king crab continues into adulthood. A common assumption is that adults are not podding crab. I present data from in situ investigations at Kodiak and adaptive cluster sampling in Bristol Bay, which demonstrates that adults are podding crab whose behavior results in discrete aggregations that can cover more than 370 km<sup>2</sup>. Because of this behavior, and because historical estimates of precision were based on a flawed method (post-stratification), the uncertainty of annual abundance estimates, and their association with climate changes, is greater than previously thought.

# Introduction

Podding is an intensely gregarious behavior unique to red king crab (*Paralithodes camtschaticus*) (Dew 1990, Dew et al. 1992, Dew and McConnaughey 2005). The behavior causes the crab to be spatially distributed throughout the year in extremely dense clusters or aggregations known as pods. Unlike the transitory mating and molting aggregations of sexually mature crab reported for several species in

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the family Majidae, e.g., spider crab (*Libinia emarginata*) (Degoursey and Stewart 1985, Degoursey and Auster 1992), opilio crab (*Chionoecetes opilio*) (Hooper 1986), lyre crab (*Hyas lyratus*) (Stevens et al. 1992), and Tanner crab (*Chionoecetes bairdi*) (Stevens et al. 1994), red king crab podding is the persistent, year-round, day-to-day, social functioning of cohesive, identifiable population units composed of juvenile, subadult, and adult red king crab of both sexes. While the quotidian aspect of red king crab podding distinguishes it from the occasional aggregative behavior observed for other crab species, it also results in populationabundance estimates that are considerably less precise than equivalent estimates for other major crab (Tanner and opilio crab) and fish (walleye pollock [*Theragra chalcogramma*], Pacific cod [*Gadus macrocephalus*], and yellowfin sole [*Limanda aspera*]) species targeted by the annual NMFS multispecies bottom-trawl survey of the eastern Bering Sea (Dew and Austring 2007).

Early research resulted in a circumscribed definition of podding behavior that led to the misconception that adult red king crab do not form pods. For example, Powell and Nickerson (1965) defined a pod by its size (no more than 3,000 crab), shape (spherical), and activity (resting). Under this definition, foraging aggregations were not pods; and adults, which had been observed to form piles or aggregations but not "spherical" pods, were assumed to have outgrown their podding behavior early in their fourth year of life (age 3). However, trying to define a pod (or a flock, herd, or school) solely by its structure rather than its function (e.g., social organization) has not proven to be particularly useful. Also, Powell and Nickerson's (1965) definition was based on daytime-only observations of a pod's resting phase—observations that led them to conclude, incorrectly, that the observed pod remained in the same location for days or even weeks without foraging. Some 25 years later the discovery of a diel podding cycle, whereby the crab dispersed from the resting pod each evening, foraged as a cohesive unit throughout the night, and reconstituted the resting pod each morning (often in the same location), revealed the structural fluidity and organizational persistence of podding behavior (Dew 1990). Now it could be understood that a pod has a continuously changing structure, and that pod members often alternate each day between a resting phase and a foraging phase, with little to be gained by differentiating among piles, pods, and aggregations (e.g., Powell and Nickerson 1965, Stone et al. 1993), all of which may be manifestations of the same, cohesive population unit.

Based largely on Powell and Nickerson (1965), a consensus hypothesis underlying the management of the Bristol Bay red king crab stock is that podding is specific to juveniles only, and that podding behavior ceases after red king crab attain a size of 60-65 mm CL at age 4 (e.g., Incze et al. 1986, Otto 1986, Armstrong et al. 1993, Witherell 1998, Ackley and Witherell 1999). The question of whether podding continues into adulthood is of more than academic interest. Incze et al. (1986, p. 375) commented that if adult red king crab were podding crab, "a tremendous sampling effort would be required to obtain reasonable estimates" of their abundance, suggesting that the precision of population estimates based on sample sizes typical of the NMFS Bristol Bay survey might be unacceptably low for podding crab.

The consensus hypothesis implies that red king crab discontinue podding and disperse to a more tractable, less aggregated spatial distribution at about the time they become a target of the NMFS stockassessment survey as subadult and adult crab. This is the hypothesis favored by resource managers responsible for estimating red king crab abundance each year. Consistent with this hypothesis, Otto (1986) reported rather precise 95% confidence intervals of ±12-27% for abundance estimates of legal crab (males with carapace length (CL)  $\geq$ 135 mm) in Bristol Bay during the years leading to the collapse of the stock (1975-1983). Because podding is associated with low abundance-estimate precision, investigators (e.g., Incze et al. 1986, Armstrong et al. 1993) interpreted the relatively high precision reported by Otto (1986) as evidence that adults, unlike juveniles, are not podding crab. However, overlooked by investigators is the fact that the precision reported for adult red king crab was inflated by an invalid stratification method: "In each year . . . this area is stratified on the basis of large [red king crab] males . . ." (Otto 1986, p. 93). This method, known as post-stratification, is a scheme in which stratum formation is based on the spatial distribution of the survey target as determined from the current year's sampling. Post-stratification is a form of data mining that results in an artificially low estimate of variance that is unsuitable for calculating a useful estimate of precision (Cochran 1977, Hilborn and Walters 1992, McConnaughey and Conquest 1993, Gunderson 1993, Skalski 1997).

According to the consensus hypothesis, red king crab engage in podding behavior temporarily, for a 2- to 3-year period during their 15-20 year life span. However, the inception of podding at about 1.5 years of age (Powell and Nickerson 1965, Dew 1990) represents a sharp, apparently advantageous, discontinuity in the behavioral ecology of juvenile red king crab. Pre-podding, early benthic–phase juveniles display a cryptic, solitary existence that is behaviorally distinct from older, podding individuals (Loher 2001). Podding juveniles, no longer reliant on complex habitat to provide individual niches for protection, expand their foraging time and space to include daylight hours and featureless silt or mud bottoms (Dew 1990, 1991). Implausibly, the consensus hypothesis proposes that age-4, subadult red king crab abandon their newly adopted podding strategy and revert to less organized, more solitary behavior, shortly before they attain sexual maturity and begin to reproduce.

The objective of this work is to present evidence that disproves the long-held hypothesis that podding is strictly a juvenile phenomenon, dwindling to insignificance after age 3. Instead, the intensity of podding appears to increase as discrete cohorts, approximately midway through the fourth and fifth years of life (age 3-4), proceed to mix and coalesce into a single, larger, multi-age aggregation (Dew et al. 1992). Once we accept the evidence that adult crab are highly aggregated podding crab, we are faced with the Incze et al. (1986) observation that it is extremely difficult to obtain reasonably precise abundance estimates for podding crab. In turn, we might begin to suspect that the confidence intervals published since 1975 are overly precise, and that red king crab abundance estimates presented to and used by managers are likely to be more uncertain and unreliable than claimed. Finally, we should reevaluate all analyses and conclusions that rely on and assume reasonably precise abundance estimates—e.g., stock-recruitment relationships (e.g., Zheng et al. 1995), the calculation of utilization rates (e.g., Dew and Austring 2007), and the effect of climate change on abundance (e.g., Tyler and Kruse 1996).

# Methods

#### Kodiak

Observations of red king crab podding behavior were made in situ by divers during a 12-year (1985-1996) study focused primarily on Womens Bay (57.7208°N, 152.5250°W), a 490-hectare embayment contiguous with Chiniak Bay and the Gulf of Alaska, and 14.5 km south of the city of Kodiak, Alaska. Most of the dive effort was directed to Womens Bay because information from a 1990-1991 study showed red king crab to be substantially more abundant there than in two other local bays (e.g., Anton Larsen Bay and Trident Basin) (Dew 1991). Investigators used scuba to locate crab pods, and then tagged one or two pod members with a sonic pinger to track the pods from a small boat equipped with a directional hydrophone and a global positioning system receiver. To forestall the possibility that investigators were either tracking a few tagged stragglers instead of thousands of podding crab, or dealing with stationary tags shed during the winter molt and lying on the bottom, divers made frequent, in situ observations to document the behavior of the pods and to periodically collect (and replace) podding crab for length measurements, from which crab ages were estimated. Observations and counts were recorded on writing slates during the dive, and depth profiles were recalled from diver-carried computers that recorded depth at three-minute intervals. Data from more than 500 dives (>280 hours underwater, including approximately 50 hours of night diving) provided information with which to define diurnal and seasonal activity cycles and foraging habits, and to quantify seasonal variations in depth, habitat usage, mobility, dispersion, mixing, and year-class integrity of the aggregations. Additional details of this multiyear study can be found in Dew (1990, 1991) and Dew et al. (1992).

#### **Bristol Bay**

The NMFS annual survey in Bristol Bay and adjoining waters (to 166°W) collects bottom-trawl samples at approximately 120 geographically fixed stations, each representing a grid square of 1,372 km<sup>2</sup> (400 nm<sup>2</sup>). Although commercial-size (legal) male red king crab have been collected since 1975 at some 117 of 120 regularly sampled Bristol Bay stations east of 166°W, only 24 of these stations have produced legal males more than 80% of the time (in at least 20 of 24 years) from 1975 through 1998. The location, starting point, and time of sampling are nonrandom, remaining approximately the same from year to year.

The sampling is designed to be unstratified and distributed systematically (evenly) over a uniform grid of stations, but this design is often unbalanced by nonrandom sampling that directs extra effort to areas of high crab abundance. These ad hoc, extra samples, sometimes resulting in more than twice the total number of design-based samples (Table 1), are included in population-size estimates. From as early as 1975 (Reeves 1975, Pereyra et al. 1976, Reeves et al. 1976) through at least 2008 (Chilton et al. 2008), NMFS has employed post-stratification to address the analytical complications that result from unbalancing the systematic design with extra sampling. NMFS stratification is an a posteriori stratification of the sampling area after each year's survey, using knowledge of the target species' spatial distribution in the current survey to define the strata; but then NMFS uses the standard formula for a priori stratification to calculate variance, as follows:

 $Var(\bar{x}_{str}) = \frac{a_1^2 \left(\frac{s_1^2}{n_1}\right) + a_2^2 \left(\frac{s_2^2}{n_2}\right) + \ldots + a_i^2 \left(\frac{s_i^2}{n_i}\right)}{(\sum a_i)^2}$ 

where  $\bar{x}_{str}$  = the stratified arithmetic mean density (crab per km<sup>2</sup>),  $a_i$  = the area (km<sup>2</sup>) in stratum *i*,  $s_i^2$  = the variance in stratum *i*, and  $n_i$  = the sample size in stratum *i*. Additional details of the Bristol Bay crab survey can be found in Chilton et al. (2008). Also, Otto (1986, p. 93) describes the process of "gerrymandering" strata after a survey, based on red king crab catches in the same survey.

#### Adaptive cluster sampling

The adaptive cluster sampling (ACS) conducted in 1995 was part of a bottom-trawl special study, which sampled on a relatively fine scale (3.7

Table 1. As part of the NMFS Bristol Bay trawl survey to estimate red king crab abundance, extra trawl sampling was conducted in areas of relatively high legal-male abundance during a period of apparently increasing abundance, after which the population collapsed.

Year	Ν	n	Extra tows (%)
1975	77	77	0
1976	80	137	71
1977	77	98	27
1978	82	124	51
1979	82	190	132
1980	82	95	16

N = number of grid squares (stations).

n = number of tows (samples) at the stations.

km intervals) within a 27,440 km<sup>2</sup> area of Bristol Bay (Fig. 1). In the 1995 experiment, each of 20 Bristol Bay standard-survey grid squares (37 by 37 km) was subdivided into a 10 by 10 grid yielding 100 possible sampling units (3.7 by 3.7 km). Three of these 100 units were selected randomly from an initial grid square, and this triplet was replicated throughout the remaining 19 grid squares, resulting in a total of 60 ACS sampling units, each to be sampled by a single tow of 30 minutes duration. The "neighborhood" of each of these units was defined as the adjacent units to the north, south, east, and west. If the number of red king crab caught at a unit was equal to or greater than a predetermined threshold value (C), then the unit's neighborhood was added to the sample, and so on until a cluster of units (a network) was formed in which the boundary or edge units were less than C (Thompson and Seber 1996). The initial choice of C = 18 adult egg-bearing females was based on data from the standard survey, which had passed through the 20-station ACS survey area several days earlier. The ACS emphasis on females was a response to a lack of mature females in two previous NMFS standard surveys—a lack that, despite being an artifact of survey timing (Dew 2008), caused the cancellation of the Bristol Bay red king crab fishery in 1994 and 1995.

#### Statistics

#### Checking and recalculating confidence intervals

By 1992, it was evident that there were inconsistencies between the extremely clumped spatial distribution of the crab, as observed in situ, and the rather precise estimates of their (post-stratified) Bristol Bay abundance, as published by NMFS (e.g., Otto 1986). For each year from 1975 through 1980, I checked the confidence level of the pub-



Figure 1. The 1995 Bristol Bay adaptive cluster sampling, with 60 sampling stations shown as open circles and crab aggregations shown as small points. The largest aggregation at F13 was continuous over more than 90,000 acres. The dotted line shows where, after the F13 encounter, investigators increased the threshold value from C = 18 to C = 60 egg-bearing females.

lished intervals (e.g., Abell et al. 1999) by resampling the NMFS trawl survey data, rebalanced to account for extra sampling (e.g., Dew and McConnaughey 2005, Table 2). For each random resample I obtained the mean and then constructed symmetric intervals of the same  $\pm$  percent width (relative to the mean) as the published intervals. After repeating this operation 3,000 times, I calculated the proportion of these symmetric intervals that failed to include the "population" mean of the original sample. This proportion was an estimate of  $\alpha$ , the type I error rate (nominally  $\alpha = 0.05$ ); conversely,  $1 - \alpha$  was an estimate of the confidence level or quality of the interval. If the confidence level of the published interval proved to be much less than the 95% routinely stated by investigators, then the interval was unrealistically precise (too narrow).

Next, in order to determine the effect of post-stratification, I calculated symmetric 95% confidence intervals for each of 3,000 random resamples from the unstratified (but rebalanced) NMFS data. The average limits of these 3,000 intervals formed a symmetric confidence interval, which was then evaluated as to confidence level, as outlined above.

Finally, because symmetric normal-based 95% confidence intervals fail to cover the means of highly skewed catch distributions more often than the expected 5% of trials (Mandel 1964), I used Efron's original percentile method (Efron and Tibshirani 1993; Mooney and Duval 1993; Manly 1997, p. 339) to evaluate the improvement that might be gained by using asymmetric vs. symmetric confidence intervals. To do this, I again resampled the rescaled data to obtain 3,000 resample means. Using a sorted list of the 3,000 resample means for each year, a count up 2.5% to the 75th lowest value and down 2.5% to the 75th highest value gave the endpoints of a 95% bootstrap confidence interval for the mean estimated from the trawl survey.

#### Randomization tests

I used 5,000-trial randomization tests (Manly 1997) to test whether the legal-male red king crab population size was changing significantly (P < 0.05) year-over-year during 1975-1980, and whether significant differences existed among any of the 15 year-pairs between 1975 and 1980. Unlike *t*-tests or ANOVA, randomization tests are valid even when sampling is nonrandom, data are non-normal, variances are heterogeneous among years, and independence of observations is suspect (Prager and Hoenig 1989).

### Results

#### Disproving the consensus hypothesis

#### Kodiak

In situ research on the diel activity and foraging dynamics of podding red king crab at Kodiak, Alaska, during 1987-1993 led to the conclusion that most age 1-6 red king crab exist as pod members. For example, of the 11,600 age 2-3 crab counted in 1990-1991 during a 116-dive census in Womens Bay (Dew 1991), 97% were found in aggregations of  $\geq$ 500 crab. Of the estimated 101,000 age 4-6 crab observed in 1993 (36 dives, January-September), 98% were found in aggregations of  $\geq$ 1,000 crab. These data indicate that podding behavior continued and may have even intensified as the crab grew beyond age 3.

In 1990, investigators at Kodiak began to affix sonic tags to the carapaces of crab from the 1987 and 1988 cohorts (Dew et al. 1992). While tracking the crab and observing them in situ over the next several years, it became clear that red king crab continued their highly aggregative podding behavior until at least age 6, when they moved out of Womens Bay to waters >100 m deep, well beyond diving depths. Rather than becoming more randomized with time, as suggested in the litera-



Figure 2. Composite photo showing the similarity between a juvenile resting pod of age-1 red king crab (left) and one composed of adult and subadult crab estimated to range between ages 5 and 12. The juvenile pod of 500-800 crab, each about the size of a U.S. fifty cent piece (30-40 mm CL), is about 0.5 m high. The adult/ subadult pod, estimated to contain 8,000-10,000 crab ranging in size from 60 to 165 mm CL (mean = 103 mm CL), is about 2.5 m high. (Photos by B. Dew.)

ture (Incze et al. 1986, Otto 1986, Dew 1990), their distribution over the grounds grew more contagious as the discrete cohorts, approximately midway through their fourth and fifth years of life (age 3-4), proceeded to mix and coalesce into a single, larger aggregation (Dew et al. 1992).

Direct evidence that podding behavior continues into adulthood can be seen in a composite photograph (Fig. 2) documenting the similarity between juvenile and adult resting pods, where the primary difference between the two is the scale of the phenomenon. This photograph modifies the observation by Stone et al. (1993, p. 755) that "Adult pods were not similar to pods of juveniles. [Adult] pods were typically asymmetrical, and crab were usually stacked only three or four individuals deep." Because adult red king crab spend considerably more of their time foraging than resting (Dew 1990), evidence for the adult resting phase is rare compared to that for juveniles (Fig. 2 is the only known photograph of a multi-age, mixed-sex, resting pod of adult and subadult red king crab). The pod was photographed at midday on 26 September 1993 in Chiniak Bay (57.7445°N, 152.4227°W) at a depth of 22 m. The numbers of male (48%) and female (52%) crab were nearly



Figure 3. Members of the (Fig. 2) adult resting pod, now in foraging mode, moving directionally in a tight group, similar to the foraging behavior documented by Dew (1990) for podding juveniles. Note the sharp delineation between areas of high and low (no) density, a behavioral feature that contributes to the low precision of abundance estimates from the NMFS Bristol Bay trawl survey. (Photo by B. Dew.)

equal, and the mean size of the crab was 103 mm CL. The average male was 110 mm CL (range 79-165 mm), and 21% were  $\geq$ 123 mm CL, which is the size reported for males of grasping pairs at Kodiak (Powell et al. 1973). Females averaged 96 mm CL, and 12% were carrying uneyed egg clutches. The egg-bearing females ranged in size from 99 to 131 mm CL. This resting pod was only a portion of the entire aggregation, which I previously estimated to be 20,000-30,000 crab on 9 September while still in Womens Bay (57.7262°N, 152.4825°W) but moving toward the more open water of Chiniak Bay.

Rather than dispersing over a wide area when foraging, an adult pod forages as a tightly knit, single-layer unit, maintaining a distinctly contagious distribution delimited by sharp transitions from approximate densities of >5 crab per m<sup>2</sup> to densities of 0 crab per m<sup>2</sup> (e.g., Fig. 3). The movement of such "knife-edges" into or out of a fixed sampling location (e.g., the fixed sampling stations of the NMFS Bristol Bay survey)



Figure 4. Distribution of catches within aggregations at stations E10, E11, F12, F13, and G11, where predetermined threshold values were triggered. Low threshold values are likely to find even small aggregations but may be impractical given the size of the larger aggregations.

would be an abrupt, all-or-none phenomenon, likely to be interpreted as a profound change in abundance instead of a minor change in location.

#### Bristol Bay

There are no direct, in situ observations of podding behavior in the southeastern Bering Sea, either for juvenile or adult red king crab, nor have any NMFS studies been designed to make such observations. The standard NMFS assessment survey, with its grid-square arrangement of trawl stations spaced at regular 37 km intervals and collecting a single 0.04-0.05 km<sup>2</sup> sample every 1,372 km<sup>2</sup>, is likely to be a coarse sieve with which to capture a relatively small-scale phenomenon like podding (Vining and Watson 1996).

More useful was the adaptive cluster sampling (ACS) conducted in 1995 and designed to sample rare, clustered populations (Thompson and Seber 1996) with distributions similar to that expected for podding red king crab. This NMFS special study sampled on a relatively fine scale (3.7 km intervals) to reveal the nonrandom spatial distribution of red king crab in a 27,440 km<sup>2</sup> area of Bristol Bay (Fig. 1). The adaptive survey began on 10 June 1995 within grid square D10, and by 13 June, at grid square F13, the survey had encountered an aggregation so large that the



Figure 5. Length composition of 4,750 red king crab within the F13 aggregation: the highest-density catch (top), the second-highestdensity catch (mid), and the remaining 25 catches combined (bottom).

threshold value of C = 18 was still being triggered after 27 tows and several days of sampling (Fig. 1). Sampling was abandoned before the boundaries of the F13 aggregation were established, but even this incomplete sampling showed the presence of a continuous distribution of crab over an area of 370 km<sup>2</sup>, or more than 90,000 acres. Because 85% of the 27 tows within the F13 aggregation met or exceeded the initial threshold value of C = 18, the criterion was increased to C = 60 to reduce the chances of getting stalled for several days in another aggregation. Even with a *C*-value more than three times the original, the adaptive survey encountered a second large aggregation at grid square G11, 83 km to the northwest of F13, where 16 tows were completed before the effort to define the boundaries of the aggregation, now continuous over an area of 219 km<sup>2</sup>, was abandoned because of time constraints.

To set meaningful and practical *C*-values, it would help to know the catch distribution within aggregations encountered in past surveys. Based on the 1995 results (Fig. 4), a criterion of C = 18 was useful because even small aggregations were discovered; but it was impractical given the resources allocated to the study. The criterion of C = 60, while more practical, probably would not have discovered the aggregation at E10 (Fig. 1), where the highest catch in 12 tows was 20 mature females.

Of the 11,470 crab collected in 117 ACS trawl samples, 78% were from aggregations occupying grounds that represent only 3% of the total sampling area. Of the 5,768 adult crab collected, 82% were from aggregations, and more than half (53%) of the crab in aggregations were adults (males  $\geq$ 120 mm CL, females  $\geq$ 90 mm CL, e.g., Zheng et al. 1995). The average density of aggregated adults (1,360 per km<sup>2</sup>) was three times the average density of non-aggregated adults (438 per km<sup>2</sup>). The largest aggregation, encountered at F13 with an average density of 4,074 per km<sup>2</sup>, was estimated to include more than  $1.5 \times 10^6$  adult and subadult crab within the area sampled. Another large aggregation at G11, with an average density of 4,614 per km<sup>2</sup>, was estimated to include more than  $1.0 \times 10^6$  crab. These estimates understate the number of red king crab in the aggregations at F13 and G11 because sampling was halted before the boundaries of these large aggregations were ascertained.

Length-frequency analysis indicates that the size variation within aggregations was less than the variation between aggregations. The length-frequency distributions within the F13 aggregation were bimodal, with a male-female mode at 70-90 mm and a female mode at 110-150 mm (Fig. 5). These modes were present in each of the two largest F13 catches, which were 5 km apart, and in the remaining 25 F13 catches combined. The G-11 aggregation was distinguishable by its single, male-female mode at 85-120 mm, which was present in each of the two largest catches (4 km apart) and in the remaining 14 catches combined (Fig. 6). Distinctive length-frequency signatures



Figure 6. Length composition of 3,312 red king crab within the G11 aggregation: the highest-density catch (top), the second highest density catch (mid), and the remaining 14 catches combined (bottom).

throughout each of these two large aggregations, indicating that the crab were well-mixed within but not between aggregations, suggest that each aggregation was a demographically discrete, nonrandom subset of the red king crab population within the ACS area.

#### Precision

The high levels of precision reported for red king crab abundance estimates are inconsistent with data and observations indicating that Bristol Bay adult, subadult, and juvenile red king crab are podding crab whose behavior results in extremely clumped, contagious spatial distributions. Re-evaluation of the NMFS post-stratified confidence intervals using resampling methods demonstrated that the post-stratified intervals, averaging  $\pm 18\%$  of the mean during 1975-1980 (Otto 1986), overstated the precision of abundance estimates to a degree that may have adversely affected the management process. Comparable symmetric intervals without post-stratification, averaging  $\pm 39\%$ , were more than twice as wide as the NMFS intervals, and asymmetric bootstrap intervals were, on average, -35% to +44% (Table 2).

Confidence intervals that are too narrow to be realistic will fail to achieve the confidence level claimed by investigators (e.g., 95%). I used resampling methods (e.g., Abell et al. 1999) to demonstrate that the confidence level of the NMFS-published (post-stratified) intervals was closer to 60% (range = 50-73%) than the stated 95% (Table 2). Of the 3,000 confidence intervals for the resampled means ( $\bar{x}$ ), the proportion that did not include the original sample mean ( $\hat{\mu}$ ) ranged from 27% to 50%, or 5 to 10 times the  $\alpha$  = 0.05 error rate expected for 95% confidence

stratifica (15) and foil stratifica (15) intervals.									
	NMFS Poststratified (PS) <sup>a</sup>			No Stratification <sup>a</sup>			Bootstrap <sup>b</sup>		
Year	±%	α	1 - α	±%	α	1 - α	-%	+%	
1975	15	0.39	0.61	34	0.08	0.92	33	36	
1976	16	0.35	0.65	33	0.11	0.89	29	39	
1977	20	0.27	0.73	34	0.09	0.91	32	38	
1978	27	0.31	0.69	50	0.11	0.89	43	58	
1979	13	0.49	0.51	35	0.10	0.90	33	42	
1980	15	0.50	0.50	46	0.08	0.92	40	50	
Avg	18	0.39	0.61	39	0.10	0.90	35	44	

Table 2. Comparison of three types of confidence interval. Interval widths are expressed as  $\pm\%$  of the mean (legal-male density). Actual (vs. nominal)  $\alpha$ -levels, and interval quality (1 –  $\alpha$ ) are shown for post-stratified (PS) and non-stratified (NS) intervals.

PS interval widths ( $\pm$ %) from Reeves (1975), Pereyra et al. (1976), Reeves et al. (1976), Otto (1981, 1986), and Larkin et al. (1990).

<sup>a</sup> Normal-based intervals. Nominal rates:  $\alpha = 0.05$   $1 - \alpha = 0.95$ 

<sup>b</sup> Asymmetric intervals based on resampling from rescaled data.



Figure 7. Trends in population size, harvest, and effort, 1970-1983. The 1970-1980 harvest trend can be approximated by the relationship  $H_t = 2.22 \times 10^6 e^{0.24t}$  ( $r^2 = 0.986$ ), where  $H_t =$  the harvested number of crab in year t (with 1970 being t = 0). This represents a doubling of the harvest every 2.9 years. There were no significant ( $p \le$ 0.05) differences among population estimates during 1975-1980 (survey data by tow not available for years prior to 1975).

intervals. Thus, instead of the stated 1-in-1/ $\alpha$  (1-in-20) chance that the confidence interval for an estimate of mean crab abundance was wrong (i.e., that it failed to include  $\hat{\mu}$ ), there was an average 1/0.38 or a 1-in-2 to 1-in-3 chance. Clearly, there was more uncertainty associated with the NMFS population estimates than was presented to resource managers engaged in an exponential expansion of the Bristol Bay red king crab harvest during 1970-1980 (Fig. 7).

The fact that the post-stratified intervals overstate the reliability and understate the uncertainty of the NMFS population estimates, to a degree that they should not be used as an approximation of survey precision, raises the question of whether the trend of increasing population size (Fig. 7) relied upon by managers was sufficiently dependable to justify the exponentially increasing harvest during 1970-1980. Using 5,000-trial randomization tests (Manly 1997), I tested whether it was reasonable to assume that the population was increasing year-over-year during 1975-1980. Consistent with the wide, overlapping confidence intervals in Fig. 8, the randomization tests suggest that the size of the Bristol Bay red king crab population changed little, if at all, from year to



- Figure 8. Comparison of NMFS post-stratified (PS) confidence intervals with symmetric intervals without post-stratification (non-stratified, NS intervals) and 95% bootstrap (asymmetric) intervals. There were no significant differences among any of the 1975-1980 abundance estimates (open circles), although the harvest more than tripled during this time.
- Table 3. Results of randomization tests comparing densities ( $\bar{X}$ = mean number per km<sup>2</sup>, n = sample size) of legal male red king crab between consecutive years, 1975-1982. During the 1975-1980 period leading up to the population collapse, abundance did not change significantly ( $p \le 0.05$ ), although changes after 1980 were highly significant ( $p \le 0.005$ ).

Years	$\bar{X}_i$	(n) <sup>a</sup>	$\bar{X}_{i+1}$	(n) <sup>a</sup>	р	% change
1975-76	202.5	(77)	263.1	(80)	0.287	+30
1976-77	263.1	(80)	357.5	(77)	0.245	+36
1977-78	357.5	(77)	438.3	(82)	0.568	+23
1978-79	438.3	(82)	282.8	(82)	0.235	-35
1979-80	282.8	(82)	301.6	(82)	0.825	+7
1980-81	301.6	(82)	89.2	(82)	0.005	-70
1981-82	89.2	(82)	35.9	(82)	0.000	-60

<sup>a</sup>(n) is the design-based sample size; multiple tows at a station are represented by their mean.

year during the 1975-1980 period of increasing exploitation (Table 3). Not only were there no significant (P < 0.05) differences among consecutive years, there were no differences among any of the 15 year-pairs between 1975 and 1980. The only significant differences occurred as the population collapse accelerated during 1980-1982. Apparently the commercial catch swelled to record levels independent of any detectable or statistically significant change in the source population during the six years preceding its collapse.

### Discussion

An assumption of assessment surveys such as the Bristol Bay red king crab survey is that an observed trend in annual population estimates is reasonably well-correlated with a real abundance trend in the underlying population. However, without some idea of the precision of each annual population estimate, the reliability of a survey-derived abundance trend cannot be evaluated. In fact, if confidence intervals around the annual estimates are wide enough (i.e., if the uncertainty of the survey estimates is great enough), the survey-derived trend may bear little or no resemblance to the actual abundance changes in the population. In the face of high population-estimate uncertainty, there may be little chance of finding a meaningful link between climate change and abundance trends. Thus it is imperative for scientists and managers to have a full understanding of the reliability of their survey population estimates.

According to the generalized behavioral model taken from the literature, red king crab move through an ontogenetic continuum (Dew 1990) from podding juveniles with an extremely patchy distribution (Otto 1986) that requires a tremendous sampling effort (Incze et al. 1986), to age-4 crab larger than 69 mm CL that have ceased podding (Powell and Nickerson 1965, Incze et al. 1986, Otto 1986, Armstrong et al. 1993, Witherell 1998, Ackley and Witherell 1999), and on to a mature population that is "extremely amenable" to trawl surveys (Otto 1986, p. 98). Upon examination of data collected from Kodiak and Bristol Bay, it becomes clear that older red king crab (subadults and adults greater than age 4) do not conform to this model. Instead, in situ observations, photographic evidence, and the results from adaptive cluster sampling indicate that the podding behavior documented for juveniles (Dew 1990) continues into adulthood for red king crab from Kodiak and Bristol Bay. This information is consistent with the findings of Dew and Austring (2007) that red king crab, when compared to five other major species in the NMFS bottom-trawl survey of the eastern Bering Sea, occupied an extreme position within the spectrum of spatial distribution and statistical intractability, and was the species with the greatest patchiness and the lowest abundance-estimate precision.

It appears that large-scale podding of adult and subadult red king crab, rather than being a rare and unrepresentative event (e.g., Stevens et al. 1991), is a behavioral norm for the species throughout its Alaska range from Bristol Bay and Kodiak to southeast Alaska (Stone et al. 1992, 1993). This observation has implications beyond the category of interesting animal behavior. During the 1970s the red king crab fishery was the most valuable single-species fishery in Alaska, and from 1970 to 1980 the Bristol Bay harvest biomass increased steadily by more than 1400% to all-time record levels. Then, in 1981, after a male-only harvest of 130 million pounds, the Bristol Bay red king crab population abruptly collapsed in one of the more precipitous declines in the history of U.S. fisheries management. It is reasonable to assume that managers who annually recommended an exponentially increasing harvest, doubling every three years for more than a decade, were confident that the exploited population was increasing during this time. Judging from the population estimates derived from the NMFS annual stock- assessment surveys (estimates biased by repeated, nonrandom sampling in areas of high crab abundance, Table 1), the estimated number of legal male red king crab in Bristol Bay appeared to increase by nearly an order of magnitude from 1970 to 1978, after which the population began to decline (Fig. 7). However, without a realistic idea of the precision of each annual population estimate, the reliability of the late-1970s trend of increasing population size cannot be evaluated.

With respect to evaluating the precision of the 1975-1980 legalmale population estimates, the information in Table 2 provides us with three choices (not intended to be the only choices). First, we can use the published NMFS confidence intervals, averaging  $\pm 18\%$  of the mean only if we keep in mind that these are, on average, 61% intervals rather than 95% intervals. That is, the NMFS confidence intervals, biased by post-stratification, are likely to be wrong nearly 40% of the time rather than 5%, as claimed. Next, we can forego post-stratification, rebalance the sample list to account for the extra tows (e.g., Table 1), and calculate symmetric, normal-based confidence intervals. These intervals, averaging  $\pm 39\%$  of the mean and with an average confidence level of 90% ( $\alpha = 0.10$ ), are more than twice as wide as the NMFS low-quality 61% intervals. This represents a substantial improvement over the NMFS intervals, whose quality is degraded by post-stratification. Last, we can achieve some additional improvement in the quality of the intervals by accounting for the fact that typical red king crab survey data are highly skewed (non-normal), and that the precision of skewed data is better evaluated with asymmetric bootstrap confidence intervals, rather than with symmetric, normal-based intervals. The average limits of the asymmetric intervals are -35% to +44%, with a confidence level of 95% (by definition). With regard to the task of differentiating between climate change and fishing effects, we should recall that if a stock-size

estimate is highly uncertain, even less will be known about the fishing pressure on the stock. For example, using an interval width of  $\pm 40\%$  for a population-size estimate, the corresponding interval width for the utilization (harvest) rate is  $\pm 95\%$  (Dew and Austring 2007).

Understanding that the confidence intervals around the individual population estimates during 1975-1980 are on the order of  $\pm 35-50\%$ instead of  $\pm 15-20\%$  as published, it is prudent to question whether the 1975-1980 data can be used to define a trend (e.g., Fig. 7), or whether such a trend tells us much, if anything, about actual abundance changes in the underlying population. Upon statistical examination (randomization tests), there were no significant (P < 0.05) differences among consecutive years between 1975 and 1980, nor were there significant differences among any of the 15 year-pairs (e.g., 1975 vs. 1978, a period during which the population ostensibly increased by >100%). However, the statistical power of the tests was sufficient to show highly significant differences as the population collapsed after 1980. Unfortunately, the best climate data in the world might not be particularly enlightening when plotted against red king crab data points, none of which can be differentiated by statistical testing, and whose uncertainty is quantified by confidence intervals of  $\pm 35\%$  to  $\pm 50\%$ .

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