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REPRODUCTIVE BIOLOGY OF THE FEMALE BLUE KING CRAB *PARALITHODES PLATYPUS* NEAR THE PRIBILOF ISLANDS, ALASKA

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ABSTRACT

Female blue king crabs, *Paralithodes platypus,* from the Pribilof Islands, were sampled during each of four seasons to determine whether they spawn each year, as do red king crabs, *P. camtschatica,* or every other year, as reported for Asian blue king crabs. Based on seasonal changes in two indices of ovarian development (standardized ovary weight and mean oocyte diameter) we found the period between successive spawnings to be two years and the period of embryonic development to be 14–15 months. The fecundity of blue king crabs increases with size according to: $E = 241{,}629\text{–}2{,}632{,}606\ e^{-0.0280L}$, where E is fecundity and L is carapace length in mm. Mean length and width of new external eggs are 1.2 mm and 1.0 mm.

The blue king crab *Paralithodes platypus* is a large lithodid that is commercially harvested in both Alaskan and Asian waters. In the eastern Bering Sea, where the major United States fisheries occur, the blue king crab historically has contributed less to the total catch than its more famous relative, the red king crab, *P. camtschatica.* However, due to a recent precipitous decline in the abundance of the red king crab, the blue king crab is now the primary component of the catch (Otto, in press).

Although red and blue king crabs are of similar size and, except for color, of similar appearance, they may differ markedly in their reproductive biology. Red king crabs spawn annually and incubate their embryos for approximately 12 months (Marukawa, 1933), whereas, according to Sasakawa's (1973, 1975a) studies of Asian populations, blue king crabs spawn in alternate years and incubate their embryos for approximately 19 months.

This difference in reproductive biology is especially important for fishery management. One objective of crab fishery management in Alaska is to optimize the reproductive potential of each harvested population (North Pacific Fishery Management Council, 1982). To help achieve this goal, harvest is restricted to males and both a minimum legal size and a harvest rate are chosen to preserve sufficient males to mate with all receptive females. The adequacy of these measures is checked annually by examining the percentage of mature females carrying embryos. For red king crabs, this percentage has almost always been near 100%, but, for blue king crabs, it has often been considerably less. If Alaskan blue king crabs spawn in alternate years, then a low percentage of ovigerous females should not cause alarm. However, if Alaskan blue king crabs spawn each year then a low percentage of ovigerous females may indicate an overharvest of males. This study was initiated to verify that Alaskan blue king crabs spawn in alternate years and to determine whether blue and red king crabs differ in other aspects of their reproductive biology.

MATERIALS AND METHODS

The Pribilof Islands population of blue king crabs has been sampled with bottom trawls during stock assessment surveys of the eastern Bering Sea conducted by the National Marine Fisheries Service during June and July each year since 1979. Female blue king crabs obtained in each trawl haul were measured for carapace length (see Wallace *et al.,* 1949, for a description of this measurement) and

classified into one of the following categories of external reproductive condition: (1) immature—no embryos or empty egg cases attached to the pleopod setae; (2) uneyed embryos—attached embryos lacking conspicuous dark eye spots; (3) eyed embryos—attached embryos with dark eye spots; and (4) empty egg cases—attached empty egg cases. Female red king crabs from Bristol Bay were sampled at approximately the same time, in the same years, using the same methods as blue king crabs.

To augment the survey data, we began a program to sample near the Pribilof Islands during other seasons, but sampling of this remote area was conducted only as opportunity allowed. Five years were required to obtain a sample of mature females representing each of the four seasons. Sampling dates, number of specimens, and method of collection were as follows:

Date	Sample size	Sampling method
21 February 1983	74	trawl
15–30 April 1979	48	pot
5–17 July 1983	72	trawl
1–28 October 1981	71	pot

Females were measured for carapace length and classified by external reproductive condition. The ovary was then removed and stored in 10% sea-water formalin buffered with sodium borate.

Ovarian development was determined using two criteria: standardized ovary weight or ovarian index and mean diameter of developing oocytes. To calculate ovarian index, whole preserved ovaries were rinsed in fresh water, blotted dry, and weighed to the nearest g. Ovary weight was then divided by the weight of a female predicted by the weight-size equation:

$$\log W = -3.88 + 2.27 \log L \qquad (N = 67, R^2 = 0.83)$$

where W is whole body weight, less any attached embryos, in g and L is carapace length in mm.

To estimate mean diameter of developing oocytes, a 1 or 2-g sample of each preserved ovary was selected at random, placed in a petri dish containing water, and teased apart. One of three methods of choosing a subsample of oocytes was used, depending upon the apparent size distribution of the oocytes. If the distribution was unimodal and the oocytes were uniformly small, then 30 eggs were chosen. If the distribution was clearly bimodal, then 30 eggs from the largest mode were chosen. If the distribution was not clearly bimodal and the oocytes were variable in size, then 200 eggs were chosen. To eliminate potential bias to variability in egg shape, only eggs that were close to spherical were selected for the sample. Eggs were then measured to the nearest 0.1 mm using an ocular micrometer. If a small subsample was chosen, then mean oocyte diameter was calculated as the mean of all 30 measurements, rounded to the nearest 0.1 mm. If a large subsample was chosen, then an oocyte size frequency histogram was constructed. Based on the appearance of this histogram, a size was chosen that appeared to separate the modes (the low point between the two modes). Mean oocyte diameter was then calculated as the mean of all measurements greater than or equal to this size. Large subsamples were required for only 5% of the samples.

To estimate fecundity, 145 whole egg masses were collected during June and July in 1978 and 1979, and preserved in 10% sea-water formalin buffered with sodium borate. Egg masses were later air-dried, separated from pleopods and setae, and weighed to the nearest 0.1 mg. From each egg mass, two subsamples of approximately 250 eggs were weighed and counted. Fecundity was then estimated by dividing total weight of the egg mass by the mean of the two estimates of individual egg weight. To estimate external egg size, 25 egg samples were collected in June 1983 and preserved as above. Maximum lengths and widths of 20 eggs from each sample were measured to the nearest 0.1 mm with an ocular micrometer. Mean egg length and width for each crab were estimated and rounded to the nearest 0.1 mm. To compare egg size between species, 25 egg samples from female red king crabs were collected in June 1983 from Bristol Bay and processed in the same manner.

Results and Discussion

In the reproductive cycle for Asian blue king crabs described by Sasakawa (1973), a female extrudes a clutch of eggs in November and carries the embryos for approximately 19 months until they hatch in May of the second succeeding calendar year. A female then continues to carry empty egg cases attached to the pleopod setae until she molts and again extrudes eggs in the following autumn. The two main aspects of this reproductive cycle, that is, a 2-year ovarian cycle and a 19-month embryonic period, will be considered separately.

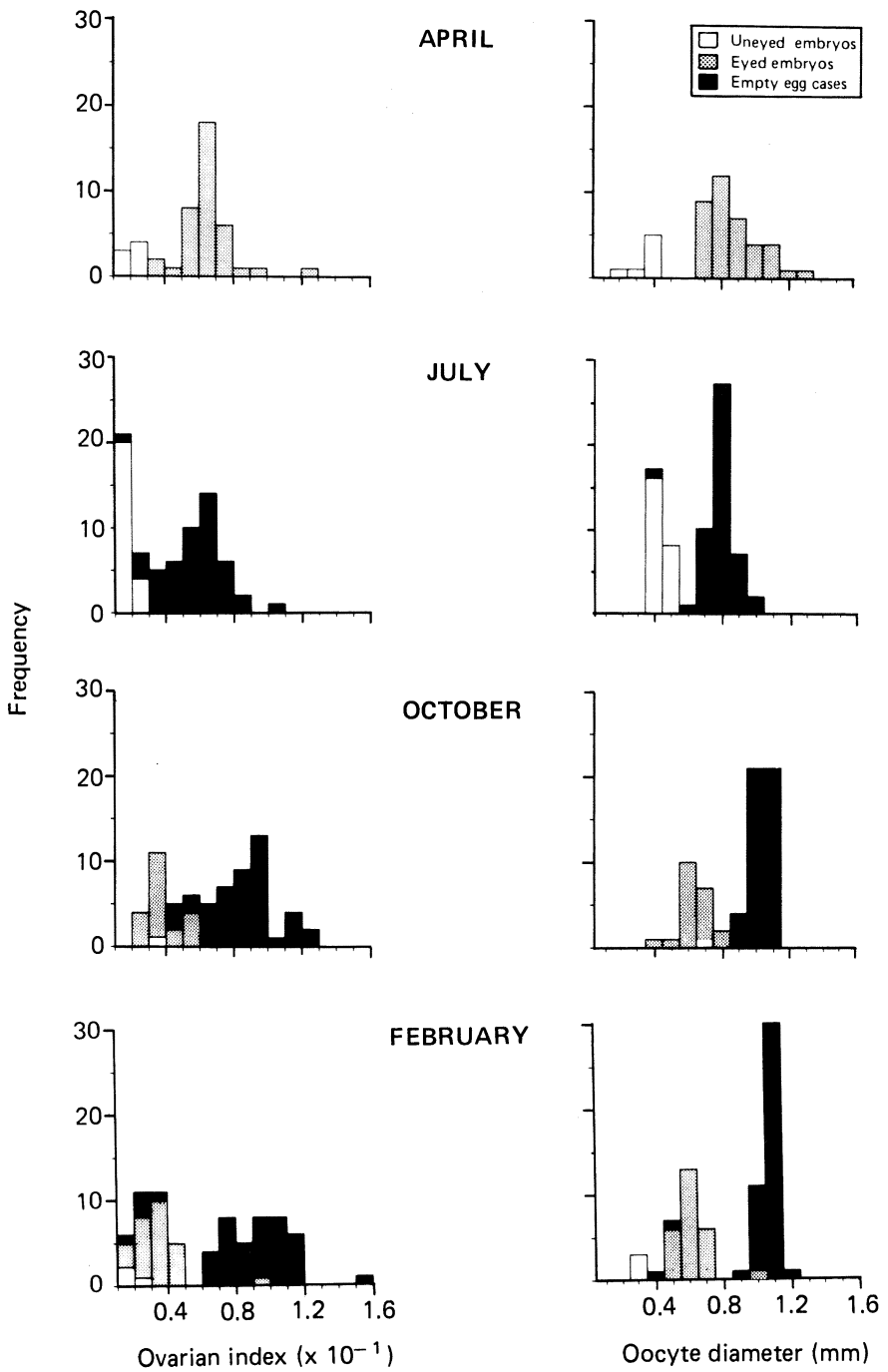

Fig. 1. Frequency histograms of ovarian index and oocyte diameter of blue king crabs classified by the three stages of external reproductive condition (uneyed embryos, eyed embryos, and empty egg cases) for each of the four sampling periods. The sequence begins in April, when egg extrusion appears to be complete.

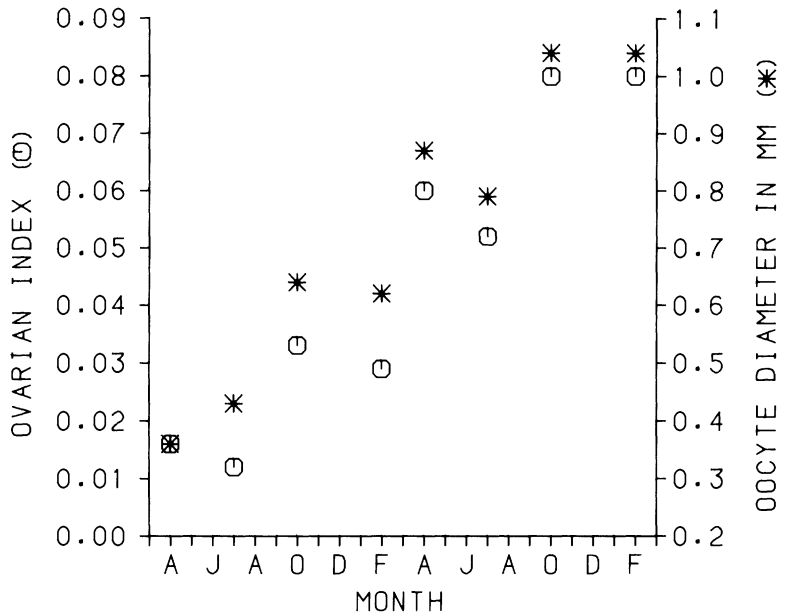

Fig. 2. Mean monthly values of ovarian index and oocyte diameter of blue king crabs for a hypothetical cohort of mature females followed over a 2-year period.

Ovarian Cycle

To determine whether Pribilof Islands blue king crabs have a 2-year ovarian cycle, we constructed frequency histograms of ovarian indices (OI) and oocyte diameters (OD), categorized by the three mature stages of external reproductive condition (uneyed embryos, eyed embryos, empty egg cases). These histograms are arranged by season (Fig. 1) beginning with April, when egg extrusion appears to be complete.

In all four seasons, both OI and OD histograms are bimodal, with the smaller mode (earlier stage of ovarian development) being composed of females in an earlier stage of external reproductive condition, measured from egg extrusion, than females composing the larger mode. This indicates that, throughout the year, the adult female population consists of two distinct groups differing both in their ovarian development and in their external reproductive condition. Such grouping is an essential feature of a 2-year ovarian cycle, and, according to Sasakawa's hypothesis, represents individuals in each of the alternate phases of this cycle.

Although our data were not collected sequentially, if the monthly values of OI and OD are assumed to be relatively constant between years, then a hypothetical cohort of females can be followed for a complete ovarian cycle, from one egg extrusion to the next. This cycle begins with females carrying uneyed embryos in April, progresses to females with eyed embryos in October, February, and April, and on to females with empty egg cases in July, October, and February (Fig. 1). When the monthly mean values of OI and OD for this cohort are plotted against time (Fig. 2), they increase almost linearly and reach the approximate midpoints of their ranges at 1 year. This indicates that ovarian development requires 2 years for completion and that the rate of development is nearly constant over this period.

Nearly all crabs sampled appear to conform to this 2-year reproductive cycle; however, some females appear to spawn two years in succession. This is seen in the February and April samples (Fig. 1) which have females with eyed embryos and exceptionally large oocytes. Since the sizes of these oocytes are similar to the size just before extrusion, these females were apparently ready to spawn for the second year in succession. Another cold-water crustacean, the American lobster (*Homarus americanus*), also spawns biennially, but this pattern is not invariant and many, if not most, individuals living in warmer areas spawn annually (Aiken and Waddy, 1980). If spawning frequency of blue king crabs is also a function of water temperature, then perhaps in other populations the incidence of annual spawning is higher than we observed at the Pribilof Islands.

In addition, some females appear not to spawn for two years in succession. This is seen in the February and July samples which have females with empty egg cases and exceptionally small oocytes. Females with similar characteristics were also found in Olga Bay, Alaska, and in nearly every case, these females were parasitized by a rhizocephalan (Johnson *et al.*, in press). We believe, however, that a rhizocephalan was not the cause of spawning failure in Pribilof Islands females because none of the 30 females examined histologically were found to be infested with the parasite. Females in both of these atypical reproductive conditions were also reported by Sasakawa (1973) for Asian blue king crabs.

Period of Embryonic Development

Besides the 2-year ovarian cycle, another important feature of Sasakawa's (1973) hypothesis is the 19-month period of embryonic development. Due to the infrequency of our sampling, we cannot precisely determine when egg extrusion and embryo hatching occur; therefore we cannot precisely determine the length of the embryonic period. However, our data are at least sufficient to estimate time intervals which bound the periods of egg extrusion and embryo hatching. Egg extrusion probably did not begin until February and was nearly complete by April, because few females with uneyed eggs were observed in February (Fig. 1) and no females with empty egg cases were observed in April. Embryo hatching had not begun by April and was complete by July because no females with empty egg cases were observed in April and no females with eyed eggs were observed in July. If the times of egg extrusion and embryo hatching are chosen to be the midpoints of their respective intervals, then the embryonic period extends from March to May or June of the following year, approximately 14–15 months.

Although this estimate is uncertain, we believe the embryonic period is shorter than the 19 months reported by Sasakawa (1973). The difference between the two estimates of embryonic period is due to Sasakawa's earlier time of egg extrusion (November). Sasakawa, however, did not collect samples during November, but, based on the large size of the oocytes observed in October, he assumed that egg extrusion would occur during the next month. We also found females with large oocytes in October, but, based on the incidence of females with uneyed embryos, it is unlikely that egg extrusion started before February. We therefore believe that Sasakawa probably overestimated the length of the embryonic period.

We also believe that the embryonic period of the blue king crab is longer than the 12-month period of the red king crab. In our April collection, we did not obtain females with empty egg cases. Except for pathological cases, females with empty egg cases in spring either have recently hatched their embryos or will soon extrude eggs. The lack of such females indicates that egg extrusion was complete (except for ovigerous females that would have extruded eggs for the second year

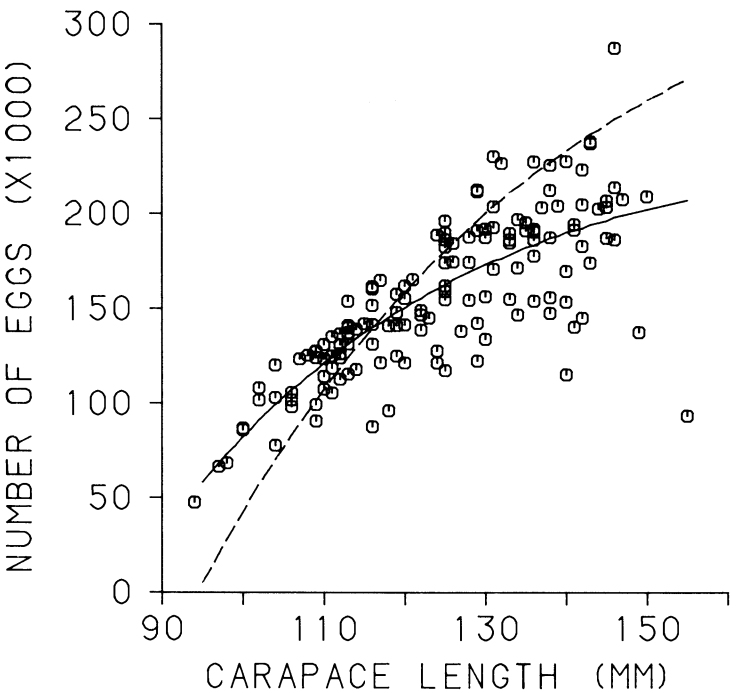

Fig. 3. Fecundity and size of 145 female blue king crabs and the fitted asymptotic fecundity-size relationship (solid line). For comparison, the asymptotic fecundity-size relationship for red king crabs is also shown (dashed line).

in succession) and that embryo hatching had not yet begun. If barren females are usually absent at this time of year [in an extensive sample collected near the Pribilof Islands in April 1984 females with either uneyed or eyed embryos were found, but barren females were not (D. Armstrong, University of Washington, Seattle, personal communication)], then the embryonic period must be longer than 12 months. An additional reason for believing that blue king crabs have an embryonic period longer than 12 months is that they have larger eggs than red king crabs (see next section) and Wear (1974) showed that, among closely related crab species, embryonic period increases with egg size. Since red king crabs have a 12-month embryonic period, blue king crabs should have an embryonic period longer than 12 months.

A 14-month embryonic period, however, appears to conflict with the observation that some females spawn in consecutive years. We do not know whether consecutive spawning is a persistent or a sporadic event in the life of an individual, but if it is the former then at least some females must have embryos that are able to complete development within 12 months.

Fecundity

Sasakawa (1975b) reported that the fecundity of Asian blue king crabs increases with carapace size at a diminishing rate; that is, the relationship is curvilinear. To determine whether this is also true for Pribilof Islands blue king crabs, a parabola was fitted to fecundity and carapace length data, using linear regression,

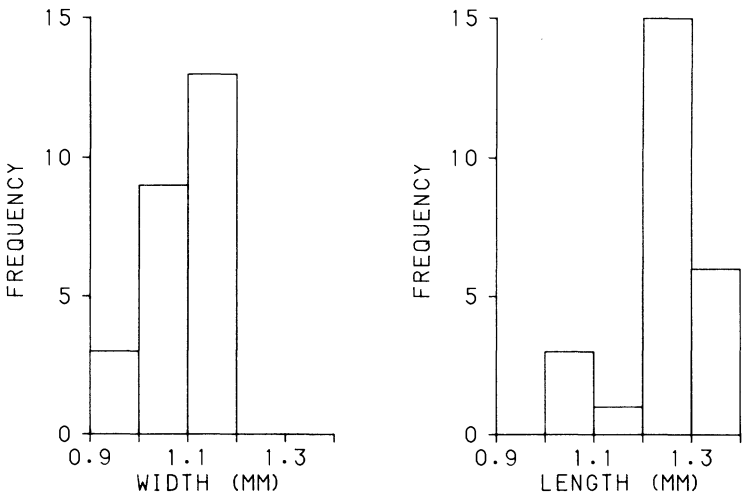

Fig. 4. Frequency histograms of the mean widths and lengths of the new external eggs of 25 female blue king crabs.

and the coefficient of the squared term was tested for significance. Since the test was significant (t test, $P < 0.05$), the fecundity-size relationship is curvilinear. For predictive purposes, however, we chose instead the asymptotic relationship proposed by Somerton (1981), $E = E_\infty - Ae^{-BL}$ where E is fecundity at size L; and E_∞, A, and B are parameters. Weighted nonlinear regression, with weights equal to the inverse of the expected variance of fecundity at each length, was used to fit this equation to the fecundity and size data. The estimated parameter values are: $E_\infty = 241{,}629$; $A = 2{,}632{,}606$; and $B = 0.028023$. Fecundity and size data and the fitted equation are shown in Fig. 3.

Egg Size

For blue king crabs, size frequency histograms of egg length and egg width are shown in Fig. 4. Mean egg length and width are 1.2 mm and 1.0 mm, close to the mean egg length and width of 1.18 mm and 0.98 mm reported by Sasakawa (1975b) for Asian blue king crabs. For red king crabs, mean egg length and width are 1.0 mm and 0.9 mm, close to the 0.97 mm mean length for red king crabs reported by Haynes (1968).

Reproductive Strategies of Blue and Red King Crabs

Within a steady state population, a female must produce, on the average, two offspring that survive to adulthood. Since blue king crabs spawn biennially, whereas red king crabs spawn annually, under the assumption of steady state populations it follows that other aspects of their reproductive strategies must also differ to allow the two species to be equal in their ability to produce reproducing offspring.

Blue king crabs could compensate for more infrequent spawning by expending more energy per spawning, that is, by producing larger eggs or more eggs than red king crabs. Egg size was compared between species using a Mann-Whitney statistic and both the length ($W = 365$, d.f. = 25,25, $P < 0.001$) and width ($W = 400$, $P < 0.001$) of blue king crab eggs were significantly larger than red king crab eggs. The larger eggs of blue king crabs are reflected in their larger larvae

[mean total length of stage I zoea: blue king crab, 4.9 mm (Hoffman, 1968); red king crab, 4.6 mm (Sato and Tanaka, 1949)]. If a larger size allows larvae either to withstand longer periods of starvation, or to include a broader size range of prey in their diet, or to avoid predators more effectively, then the survival rate of blue king crab larvae could be higher than that of red king crab larvae.

Fecundity of blue king crabs was compared to that of red king crabs using fecundity and size data given by Haynes (1968, fig. 1 data obtained using a flat bed digitizer). Although Haynes described the red king crab fecundity-size relationship with a straight line, a test for curvilinearity was significant ($P < 0.01$). The asymptotic fecundity-size relationship was fitted to the red king crab data using weighted nonlinear regression, and the fitted equation was plotted with that of the blue king crab (Fig. 3). Although blue king crabs are slightly more fecund at small sizes and slightly less fecund at large sizes than red king crabs, considering the entire size range, fecundity is not substantially different.

The egg size and fecundity information can be used to compare the clutch volume produced by equal-sized blue and red king crabs. Since the eggs of both species are ellipsoidal, the volume of an individual egg is equal to $0.75\ \pi\ (L/2)\ (W/2)^2$ where L and W are the egg length and width. Based on our estimates of mean egg length and width, egg volume is 0.628 mm^3 for blue king crabs and 0.424 mm^3 for red king crabs. Multiplying these egg volumes by the appropriate size-specific fecundities we obtained the following data:

Carapace length (mm)	Clutch volume (cm^3) blue	red	Volume ratio (blue : red)
100	51.4	18.0	2.9:1
120	94.5	67.2	1.4:1
140	119.0	98.8	1.2:1

Over their entire adult size-range blue king crabs produce a greater volume of eggs per spawning than equal-sized red king crabs. Assuming that the energetic costs of producing a unit volume of eggs is equal between species, then blue king crabs also expend more energy per spawning than red king crabs.

Blue king crabs could also compensate for infrequent spawning by having a longer adult life-span than red king crabs. Although the adult life-spans of both species are not known with certainty, for comparative purposes the relative length of the adult life-span can be estimated from adult size-range, growth increment per molt, and intermolt period. Adult size-ranges from female blue king crabs (99–144 mm) and red king crabs (84–133 mm) were estimated as the empirical 95% probability bounds (the 0.025 and 0.975 values on cumulative frequency histograms) of the adult size distributions shown in Fig. 5. (This measure of size-range is better than the minimum and maximum sizes because it is less influenced by the rare but extraordinarily large or small individiuals.) Mean growth increment per molt for mature female blue king crabs is 6.8 mm (Sasakawa, 1975b) or, using Sasakawa's correction for probable measurement bias, 5.2 mm in carapace length. Mean growth increment per molt for female red king crabs from Bristol Bay is 5.1 mm in carapace length (Weber, 1974). Since molting immediately precedes egg extrusion for both species, the intermolt period is two years for blue king crabs and one year for red king crabs. Using these values, adult longevity can be estimated from:

$$\frac{\text{(adult size-range)(intermolt period)}}{\text{(molt increment).}}$$

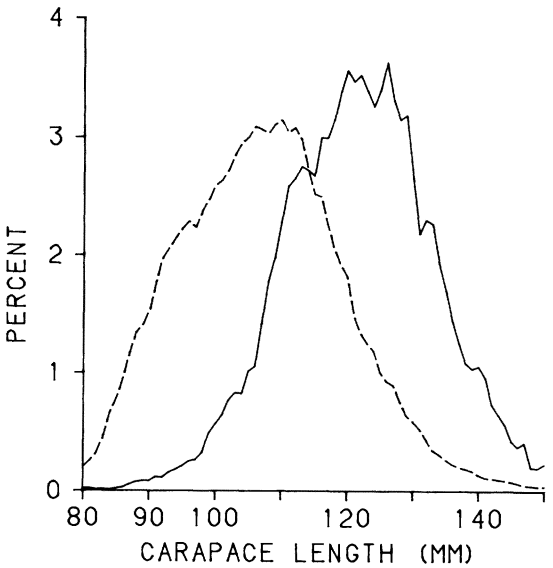

Fig. 5. Carapace length frequency of adult female blue king crabs from the Pribilof Islands (solid line) and adult female red king crabs from Bristol Bay (dashed line). Both frequency plots are unweighted averages over five years (1979–1983) of eastern Bering Sea survey data.

A female blue king crab would thus require 17 years (or, if the uncorrected growth increment is used, 13 years) and a female red king crab would require 10 years to grow from the lower to the upper 95% probability bound of the adult size distribution.

Although these comparisons are admittedly crude, they suggest that female blue king crabs expend more energy per spawning, produce larger larvae with, presumably, a higher survival rate, and have a longer adult life-span than female red king crabs. All these features tend to increase the probability of blue king crabs producing more offspring, and therefore tend to compensate for the relative infrequency of their spawning.

Blue king crabs appear to conform to the low frequency reproduction (LFR) model proposed by Bull and Shine (1979). Species with LFR are those in which populations reproduce annually but individuals reproduce biennially or less often. Typically, LFR species have an accessory reproductive activity, such as a breeding migration, and the LFR behavior appears to be a mechanism to reduce the reproductive cost of this activity. For female king crabs, molting appears to be such an accessory activity because, except for pathological cases (Johnson *et al.*, in press), adult females molt only in conjunction with egg extrusion and mating. Molting imposes two costs. First, molting requires energy that otherwise could be used for egg production. A biennially reproducing species would therefore be expected to expend more energy per spawning than an annually reproducing species, not only because energy is accumulated for twice as long but also because the energetic cost of molting is incurred half as often. Second, molting is risky. A biennially molting species would therefore be expected to live longer than an annually molting species because it is subject to the physiological stress of molting and the increased vulnerability to predators only half as often. Thus one interpretation of our observations is that blue king crabs expend more energy per spawning and live longer than red king crabs because they molt less often. Bull

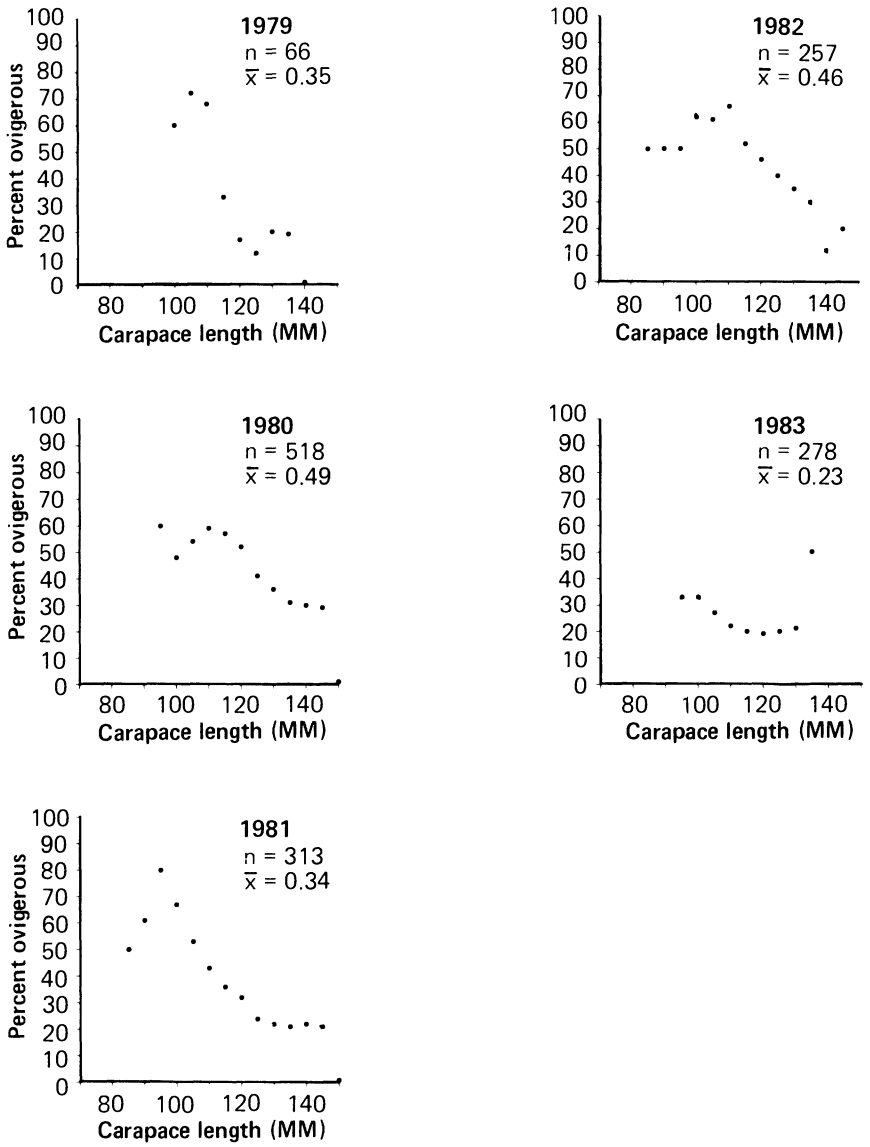

Fig. 6. Percentage of adult female Pribilof Islands blue king crabs carrying embryos shown by 5 mm increments of carapace length in each year from 1979 to 1983.

and Shine (1979) also report that some LFR species display geographic variability in the frequency of reproduction, and that lower frequency is found in the habitat of poorer quality or shorter growing seasons. Since blue and red king crabs have allopatric distributions (Otto, 1981), it is possible that blue king crabs display LFR behavior because they live in poorer quality areas.

Management Implications

For managers of the blue king crab fisheries, the importance of the 2-year reproductive cycle is that the percentage of adult females carrying embryos cannot

be used, as it is for red king crab, to determine whether or not a sufficient number of males remain in the population. This index of mating success, which is shown by 5-mm size intervals for the Pribilof Islands population in each year between 1979 and 1983 (Fig. 6), varies with the size and age distribution of adult females as well as with their past reproductive history. Such variability is too large to allow the establishment of baseline values that could be used to judge the significance of possible future changes. An additional shortcoming is that the percentage of ovigerous females does not distinguish the normal barrenness of females in the second year of their ovarian cycle from abnormal barrenness due to disease or the lack of sufficient mates. A better way of determining mating success would be to devise some method of detecting unmated females in the field. Studies on red king crabs have shown that unmated females molt normally, but either resorb their oocytes or extrude unfertilized eggs which turn opaque and slough off the pleopod setae (McMullen and Yoshihara, 1969). Similar studies on blue king crabs are needed to allow fishery managers to judge better the adequacy of their conservation measures.

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ANNOUNCEMENT

The Second International Symposium on Indo-Pacific Marine Biology will be held 22 June–9 July 1986 at the University of Guam. The program for 23–28 June includes the following morning symposia:

Behavior of marine crustaceans: Recent advances.
Ecology of marine crustaceans.
Biogeography and evolution of marine crustaceans.
Recruitment mechanisms of coral reef fish.
Introduced marine species in the Indo-Pacific.
Recent findings in *Acanthaster* biology and implications for reef management.

Contributed papers are planned for each afternoon.

Post-meeting field trips on the islands of Truk (29 June–3 July) and Ponape (4–9 July) are scheduled.

All manuscripts and/or abstracts of the talks will be published in the Bulletin of Marine Science.

The deadline for making arrangements is 1 October 1985.

Those interested should write for information to:

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