

GONAD DEVELOPMENT OF SOUTHEASTERN ALASKAN DUNGENESS CRAB, *CANCER MAGISTER*, UNDER LABORATORY CONDITIONS

Author(s): Katherine M. Swiney and Thomas C. Shirley

Source: Journal of Crustacean Biology, 21(4):897-904. 2001.

Published By: The Crustacean Society

DOI: [http://dx.doi.org/10.1651/0278-0372\(2001\)021\[0897:GDOSAD\]2.0.CO;2](http://dx.doi.org/10.1651/0278-0372(2001)021[0897:GDOSAD]2.0.CO;2)

URL: [http://www.bioone.org/doi/](http://www.bioone.org/doi/full/10.1651/0278-0372%282001%29021%5B0897%3AGDOSAD%5D2.0.CO%3B2)

[full/10.1651/0278-0372%282001%29021%5B0897%3AGDOSAD%5D2.0.CO%3B2](http://www.bioone.org/doi/full/10.1651/0278-0372%282001%29021%5B0897%3AGDOSAD%5D2.0.CO%3B2)

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

GONAD DEVELOPMENT OF SOUTHEASTERN ALASKAN DUNGENESS CRAB, *CANCER MAGISTER*, UNDER LABORATORY CONDITIONS

Katherine M. Swiney and Thomas C. Shirley

(KMS, TCS) Juneau Center, School of Fisheries & Ocean Sciences, University of Alaska Fairbanks, 11120 Glacier Highway, Juneau, Alaska 99801, U.S.A. (Tom.Shirley@uaf.edu); (KMS, correspondence) current address: National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Kodiak Fisheries Research Center, 301 Research Court, Kodiak, Alaska 99615, U.S.A. (Katherine.Swiney@noaa.gov)

A B S T R A C T

The large percentage of nonovigerous adult female crabs *in situ* gave rise to the question of whether egg extrusion occurs annually in Dungeness crabs in Alaskan waters as is reported for lower-latitude populations. Accordingly, we studied seasonal variation in gonadal development for 280 male, nonovigerous female, and ovigerous female crabs, reared in flow-through tanks from October 1997 through October 1998. Gonadosomatic indexes (GSI) were determined monthly from March through October 1998 for nonovigerous females, ovigerous females, and males. Oocyte area was also measured for females over the same period. Approximately 10 crabs from each treatment group were sampled monthly. Male GSI increased significantly over time. Nonovigerous females had significantly higher GSI and oocyte areas than ovigerous females. The GSI in October decreased significantly from the GSI in September among nonovigerous females in the laboratory and field, suggesting resorption of gonads. Most mature females do not extrude eggs annually in southeastern Alaska; however, under laboratory conditions, some females can extrude eggs in consecutive years.

Dungeness crab (*Cancer magister* Dana, 1852) is distributed from the Pribilof Islands, Alaska, to Santa Barbara, California (Jensen, 1995). Mating occurs between hard-shelled males and soft-shelled females (Snow and Neilsen, 1966). After copulation, sperm is stored in paired spermathecae and eggs are fertilized as they pass by the spermathecae during extrusion (Jensen *et al.*, 1996). The eggs form a spongelike mass, adhering to the setae on the pleopods and are brooded until hatching (Jaffe *et al.*, 1987). Dungeness crabs can store and utilize sperm for at least 2.5 years (Hankin *et al.*, 1989). In southeastern Alaska, Dungeness crabs begin mating and extruding eggs September through November. Eggs hatch from April through August, with most hatching occurring in late May and early June (Shirley *et al.*, 1987).

Dungeness crabs are generally thought to extrude eggs annually (Wild, 1983; Jaffe *et al.*, 1987), but this may not be true for Dungeness crabs in southeastern Alaska. Alaska is the northern limit of the range for Dungeness crabs, and this may affect the periodicity of reproduction. Different populations of the same species may vary in duration and frequency of reproductive cycles in different areas of their range, especially those occurring at higher latitudes (Sastry, 1983).

In California, ovaries of Dungeness crabs resumed development soon after egg extrusion, while the crabs were brooding their eggs (Wild, 1983). Ovigerous females in Alaska have significantly lower feeding rates and foraging responses than nonovigerous females (Schultz and Shirley, 1997). As a result of this greatly reduced feeding, Dungeness crabs in Alaska may not have sufficient energy to allocate to gonad production until after their eggs hatch and they resume feeding. The shorter time interval between egg hatching (May–June) and egg extrusion (September–November) may result in gonad development in alternate years.

Reproductive cycles have not been examined for males of many crustacean species. Seasonal changes in gonad development have been found in some species such as the Japanese mitten crab, *Eriocheir japonicus* de Haan, 1935 (Kobayashi and Matsuura, 1995), and *Gaetice depressus* (de Haan, 1935) (Fukui, 1993). In other species, gonad development was continuous throughout the year (Sastry, 1983). No previous study has examined seasonal changes of gonads in male Dungeness crabs.

Efficient management of crab fisheries requires knowledge of the reproduction and life history of the exploited populations. The objectives of this study, for southeastern Alas-

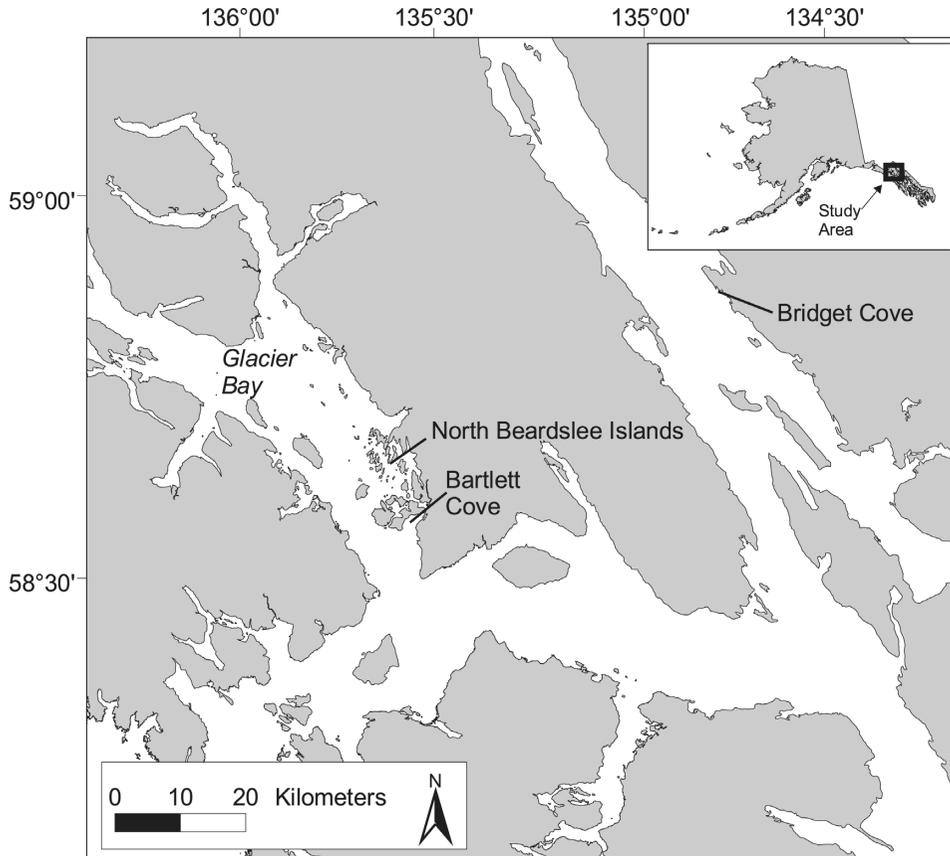


Fig. 1. Locations where Dungeness crabs were collected. Females were collected from Bridget Cove, near Juneau, Alaska. Male Dungeness crabs were collected from Bartlett Cove and North Beardslee Islands, which are within Glacier Bay National Park and Preserve.

kan Dungeness crabs were to: determine whether there is seasonal variation in gonadal development of males; compare gonadal development in ovigerous and nonovigerous females; and determine whether females extrude eggs annually.

MATERIALS AND METHODS

The majority of female Dungeness crabs were collected from Bridget Cove near Juneau, Alaska (Fig. 1) between October and November 1997, and additional females were collected from the site through October 1998. Females were collected by SCUBA, commercial Dungeness crab pots, and dip netting. Male crabs were collected from Glacier Bay National Park and Preserve, Alaska (Fig. 1) in October 1997 using commercial Dungeness crab pots. All crabs collected were measured with vernier calipers to the nearest millimeter immediately anterior to the tenth anterolateral spine; sex and reproductive state were recorded, and a numbered Peterson disk tag was attached to each crab with leg bands on the right fourth walking leg.

Crabs were held in flow-through tanks at the Juneau Center, School of Fisheries and Ocean Sciences and the

National Marine Fisheries Service, Auke Bay Laboratory. The tanks circulated sea water from 30-m depth in Auke Bay. Crabs were fed *ad libitum* a diet of fish and squid biweekly.

Only crabs that were assumed to be mature were used in this study. A histological study suggested that male Dungeness crabs are sexually mature at 109-mm carapace width (CW), and the smallest male observed in a pre-mating embrace in that study was 133-mm CW (Butler, 1960). Butler's carapace widths have been converted because he measured crabs including the tenth anterolateral spine, and for this study all crabs were measured excluding this spine. The equation used in the conversion was $y = 1.062x$ where y = carapace width including spines and x = carapace width excluding spines (Wainwright and Armstrong, 1993). All males in this study were greater than or equal to 142-mm CW. In Glacier Bay National Park and Preserve females are thought to be mature at approximately 100-mm CW, and ovigerous females were found to be greater than or equal to 106-mm CW (Swiney, 1999). All females in our study were greater than or equal to 106-mm CW.

Females were assigned to one of two groups based on their reproductive status when initially collected. Nonovigerous females at the time of collection (and that did not extrude eggs in the following months) were referred

to as nonovigerous in 1997. Female crabs that extruded eggs in 1997 were considered ovigerous in 1997. Thus, it was possible to compare gonad development between crabs that extruded eggs in 1997 and those that did not.

Crabs were held in tanks up to one year, and approximately ten crabs from each treatment group were dissected each month from March 1998 through October 1998. Crabs were randomly selected and dissected monthly. The gonads, ovaries in the females and vas deferens and testis in the males, were removed. The gonads and body were dried at 60°C to constant weight.

A total of 287 crabs were sacrificed between March 1998 and October 1998. Eighty-two males, 97 nonovigerous females in 1997, and 50 ovigerous females in 1997 were sacrificed from the laboratory. In addition, 18 males, 32 nonovigerous females, and 8 ovigerous females were collected from the field and immediately sacrificed. It was not possible to determine the recent reproductive history of these "field" females; therefore, they could not be categorized into groups based upon reproductive activity in 1997. Comparisons could only be made based upon the current reproductive status of these females. In general, the sample size of males, nonovigerous females in 1997, and ovigerous females in 1997 were 10 crabs per month except where noted (Fig. 2).

Gonadosomatic indexes (GSI) are the simplest indicator of reproductive state (Grant and Tyler, 1983a) and are useful in examining changes in gonad size over time, but are not a good predictor of developmental stage (West, 1990). Ovarian maturation is a complex process and should not be described by just one parameter (Grant and Tyler, 1983a; West, 1990). Oocyte measurements may be the best method for examining reproductive cycles in invertebrates, in part because oocyte size is independent of the size of organisms (Grant and Tyler, 1983b). A combination of gonadosomatic indexes and oocyte measurements yield a more complete picture of reproductive cycles, and both were used in this study.

Gonadosomatic indexes (GSI) were calculated by the equation:

$$\text{GSI} = (\text{gonad weight/body weight}) \cdot 100.$$

Body weight was measured after extraction of gonads, and all weights were dry weights. If a crab was missing an appendage, the same appendage from the other side was dried separately and added twice to the body weight.

Oocyte areas of female crab were measured using an image analysis program (Optimus, 1993). Preliminary oocyte measurements suggested that a sample size of six oocytes per crab is necessary to be 90% certain of detecting a 5% difference at a 5% significance level (Sokal and Rohlf, 1995). To be conservative, 20 oocytes per crab were measured. Oocyte area was measured rather than size or diameter to reduce measurement bias due to their imperfect sphericity. Microscope slides of oocytes were made by placing a small amount of gonad and one drop of glycerin on a slide, and the oocytes were immediately digitized. Preserving oocytes can change their size and shape, and thus only fresh material was used. Oocyte areas were not measured for crabs that extruded eggs in the laboratory, which were considered "spent" (Grant and Tyler, 1983b).

Statistical Analysis

Statistical methods as described by Sokal and Rohlf (1995) were used in calculations. Means, variances, and standard errors for GSI and oocyte areas were calculated

each month for males, nonovigerous and ovigerous females in 1997. The GSI values were not transformed prior to analysis. Analyses of variance (ANOVA) and Scheffé's *F* test for *post-hoc* comparisons were computed for GSI and oocyte areas among males, nonovigerous and ovigerous females in 1997 (StatView, 1996). Two-sample *t*-tests were used to detect differences between field and laboratory GSI and oocyte areas for each month that field data were available and to test for mean size differences between nonovigerous and ovigerous females in 1997 (StatView, 1996).

To determine if a significant difference occurred between nonovigerous and ovigerous females in 1997, a general linear model, similar to a 2-factor ANOVA, was used for both GSI and oocyte areas (SYSTAT, 1998). Because there was no reason to expect a similar trend in GSI or oocyte areas for the two types of females, a main effect of ovigerous and nonovigerous crabs in 1997 was not included in the model. Thus, the model contained an effect of month and tested for differences between females that were nonovigerous and ovigerous in 1997 through the interaction term for month and group.

The Pearson correlation coefficient (*r*) was used to determine if there was a relationship between oocyte area and GSI (StatView, 1996). Laboratory data were pooled and examined separately for females that extruded eggs in 1997 and those that did not.

RESULTS

In this study, male carapace width ranged from 142 mm to 198 mm, female carapace width for nonovigerous females in 1997 ranged from 106 mm to 170 mm, and ovigerous-female carapace width was 119 mm to 166 mm. No significant difference existed between the carapace widths of the two groups of females (*t*-test, *t* = 0.3, *P* > 0.05).

Gonadosomatic Index Temporal Variation

The GSI of males from the laboratory varied significantly over time (ANOVA *F* = 2.7, *P* = 0.01). The GSI generally increased March through June, reached a maximum in July and slowly decreased thereafter (Fig. 2a). The mean GSI of males from the field was significantly lower than the laboratory GSI in October (*t*-test, *t* = 2.1, *P* < 0.05), but a significant difference was not detected in September (Fig. 2a).

Laboratory females that were nonovigerous in 1997 had a significant increase in GSI (ANOVA, *F* = 11.5, *P* < 0.0001, Fig. 2b). The GSI of laboratory females in both August and September were significantly different from March, April, May and (in September only) June (Scheffé's *F*, *P* < 0.05). Significant differences also occurred between August and October GSI (Scheffé's *F*, *P* < 0.01). October GSI decreased significantly from September (Scheffé's *F*, *P* = 0.0006; Fig. 2b),

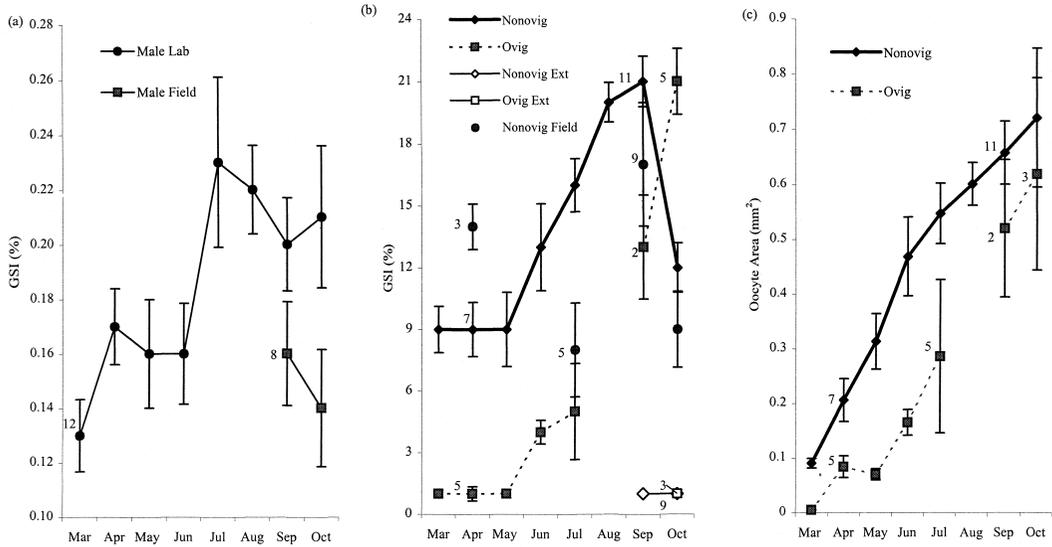


Fig. 2. Gonadosomatic indexes and oocyte areas for Dungeness crab from southeastern Alaska sampled March through October 1998. All values are means \pm one standard error. Sample size is 10 per month except as noted. (a) Gonadosomatic index (GSI) of laboratory-reared and field male crabs. (b) The GSI of laboratory-reared and field female crabs. Nonovig = females that did not extrude eggs in 1997; ovig = females that extruded eggs in 1997; nonovig ext = females that did not extrude eggs in 1997 but extruded eggs in 1998; ovig ext = females that extruded eggs in 1997 and 1998; nonovig field = nonovigerous females collected from the field. (c) Mean oocyte areas of laboratory-reared female crabs. Nonovig = females that did not extrude eggs in 1997; ovig = females that extruded eggs in 1997. Twenty oocytes were measured per crab sacrificed.

which suggests resorption of gonads because these females did not extrude eggs. October GSI also decreased from September among females from the field (t -test, $t = 2.2$, $P < 0.05$; Fig. 2b). Furthermore, the GSI of nonovigerous females from the field were significantly higher in the month of April than nonovigerous females in 1997 from the laboratory (t -test, $t = -2.4$, $P < 0.05$, Fig. 2b). Alternatively, in July, the GSI of nonovigerous females from the field were significantly lower than nonovigerous laboratory females for the same month (t -test, $t = 3.0$, $P < 0.01$, Fig. 2b). In both September and October, no significant differences were detected between nonovigerous females from the field and laboratory (Fig. 2b). The recent reproductive history of the females from the field was not known, and both females that extruded eggs in 1997 and those that did not were probably represented. Therefore, a comparison of field and laboratory females is not completely valid.

In August, 10% (5 of 50) of the nonovigerous females in 1997 extruded eggs, in September 48% (19 of 40) of the remaining females that were nonovigerous in 1997

extruded eggs, and in October 47% (9 of 19) of the remaining previously nonovigerous females extruded eggs (Fig. 2b).

Laboratory females that were ovigerous in 1997 had a highly significant increase in gonad mass through the duration of this study (ANOVA $F = 53.7$, $P < 0.0001$, Fig. 2b). Beginning in May, there was an increase in GSI that continued through October (Fig. 2b). The GSI in March, April, May, June, and July were significantly different from GSI in September and October (Scheffé's F , $P < 0.02$). The GSI were significantly different in September and October (Scheffé's F , $P = 0.02$). In October 1998, 38% (3 of 8) of the remaining females that were ovigerous in 1997 extruded eggs. These three females that were ovigerous in 1997 and extruded eggs in 1998 extruded eggs at the end of September and their GSI were calculated in October (Fig. 2b). No significant differences were found between field and laboratory ovigerous female GSI for the months of April and October.

The temporal GSI of females that were nonovigerous in 1997 was higher than the GSI of females that were ovigerous in 1997 (Fig. 2b). A general linear model, which was

Table 1. Comparison of oocyte areas between ovigerous and nonovigerous females from the laboratory and field. Top values are mean oocyte area, and values in parenthesis are standard errors. Two-sample *t*-test results are considered significant when $P < 0.05$ (*) and highly significant when $P < 0.01$ (**).

	Laboratory	Field	<i>t</i> -statistic
Ovigerous Females			
April	<i>n</i> = 5 0.84 (0.19)	<i>n</i> = 5 0.079 (0.014)	0.237
Nonovigerous Females			
April	<i>n</i> = 7 0.206 (0.39)	<i>n</i> = 3 0.335 (0.101)	-1.475
July	<i>n</i> = 10 0.547 (0.55)	<i>n</i> = 10 0.267 (0.062)	3.78*
Sept	<i>n</i> = 11 0.657 (0.56)	<i>n</i> = 9 0.514 (0.091)	1.544
Oct	<i>n</i> = 10 0.720 (0.126)	<i>n</i> = 10 0.315 (0.059)	3.643**

a modified 2-factor ANOVA, was significant in both the month effect ($F = 20.0$, $P < 0.0009$) and the interaction effect of month and whether the crab was ovigerous or not ($F = 8.2$, $P < 0.0009$). In October 1998, 47% of the remaining females that were nonovigerous in 1997 extruded eggs in 1998, and 38% of the remaining females were ovigerous in both 1997 and 1998.

Oocyte Area Temporal Variation

The average oocyte area increased over time in laboratory females that were nonovigerous in 1997 (ANOVA, $F = 17.4$, $P < 0.0001$, Fig. 2c). Mean oocyte areas in March and April differed from oocyte areas in June (March only), July, August, September and October (Scheffé's F , $P < 0.05$). Lastly, mean oocyte area in May differed from September and October (Scheffé's F , $P < 0.01$).

Field data for nonovigerous females were available for four months. Mean oocyte areas of laboratory-reared, nonovigerous females were higher than field nonovigerous females in the months of July (*t*-test, $t = 3.8$, $P < 0.01$, Table 1) and October (*t*-test, $t = 3.6$, $P < 0.01$, Table 1). No significant differences were detected between oocyte areas of nonovigerous females in either April or September.

Mean oocyte area of laboratory females that were ovigerous in 1997 increased sig-

nificantly over time (ANOVA $F = 14.6$, $P < 0.0001$, Fig. 2c). A large and constant increase in oocyte area began in June. Oocyte area in both September and October differed from March, April and May (Scheffé's F , $P < 0.05$). Oocyte areas differed between the months of March and July as well as June and October (Scheffé's F , $P < 0.05$).

Ovigerous females from the field were collected in April and October. Oocyte areas were only measured for April crabs since October ovigerous females were assumed to have recently extruded eggs. In April, oocyte areas of ovigerous laboratory and field crabs did not differ significantly (*t*-test, $t = 0.01$, $P > 0.05$, Table 1).

Mean oocyte area was lower among females that were ovigerous in 1997 in comparison to females that were nonovigerous in 1997 (Fig. 2c). A general linear model, which was a modified 2-factor ANOVA, was significant with respect to month effect ($F = 28.4$, $P < 0.0009$) and had a significant interaction effect of month and whether the crab was ovigerous or not ($F = 2.2$, $P = 0.05$).

Gonadosomatic Index and Oocyte Measurement Comparisons

Trends in GSI and mean oocyte measurements were similar for laboratory females that were nonovigerous in 1997. Oocyte area increased more constantly over time, whereas GSI remained relatively constant March through May and then began to increase thereafter. The GSI decreased sharply in October, but oocyte area continued to increase (Fig. 2b, c).

The GSI and oocyte area more closely tracked each other in laboratory females that were ovigerous in 1997. Throughout most of the study, females that extruded eggs had low GSI and oocyte area with low variance, whereas females that did not extrude eggs had higher GSI values, oocyte areas and variance (Fig. 2b, c). The GSI and oocyte area is linearly correlated for all females reared in the laboratory ($r = 0.9$, $P < 0.0001$; Fig. 3). October females that were nonovigerous in 1997 had decreased GSI and increased oocyte area and were treated as outliers and not included in the correlation.

The GSI and mean oocyte area for laboratory females that were nonovigerous in 1997, excluding October data (Fig. 3), were also correlated ($r = 0.8$, $P < 0.0001$). Likewise, the

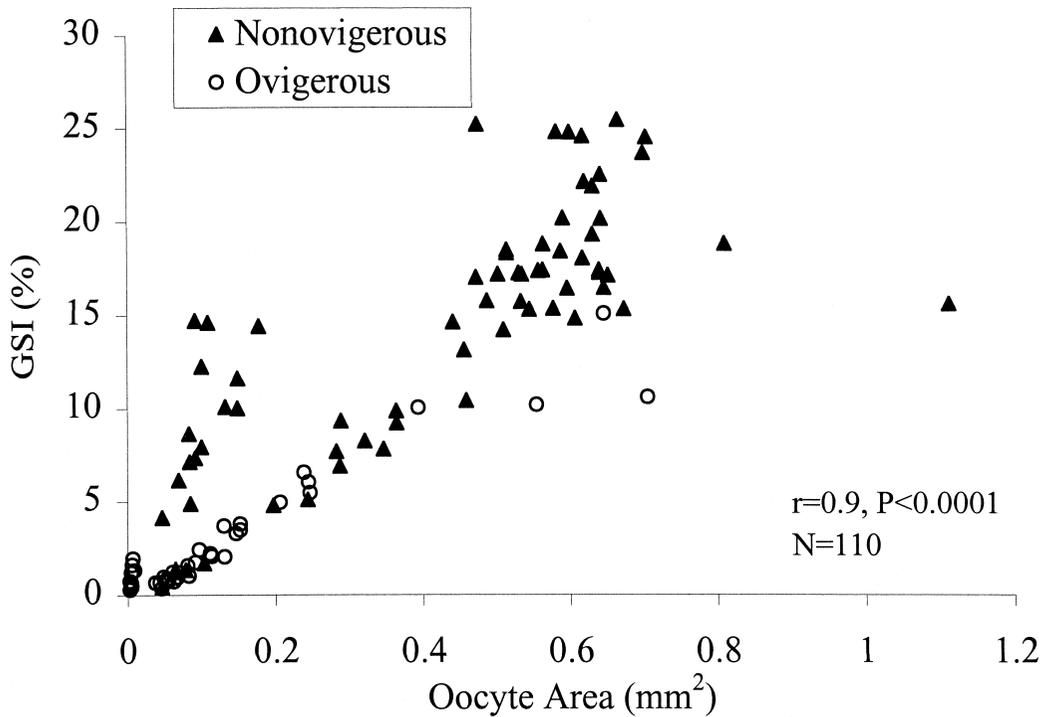


Fig. 3. Scattergram of GSI and oocyte area of females from the laboratory, excluding October data. Correlation coefficient and sample size are reported.

relationship between GSI and mean oocyte area of ovigerous females in 1997 (Fig. 3) had a high correlation ($r = 0.9$, $P < 0.0001$).

DISCUSSION

All mature female Dungeness crabs in Alaska do not extrude eggs annually. In our study, a large number of mature crabs did not produce egg clutches in 1997, and many of these extruded eggs in 1998, thus not extruding eggs in at least one year. In the laboratory, some females can extrude eggs in successive years.

Ovigerous Dungeness crabs in Alaska have reduced feeding in the laboratory (Schultz and Shirley, 1997). This reduced feeding behavior may have resulted in some mature females not extruding eggs annually. Ovigerous females may not have enough energy intake or reserves for vitellogenesis until after egg hatching when they resume feeding. In this study, eggs hatched at the end of May, and thereafter GSI among females increased (Fig. 2b).

In our study, significant differences in GSI and oocyte measurements between laboratory females that were nonovigerous and ovigerous in 1997 strongly suggest that egg extru-

sion does not occur annually in southeastern Alaska for individual females. Similar conclusions have been derived for other crab species including the false southern king crab, *Paralomis granulosa* (Jacquinot, 1852) (Lovrich and Vinuesa, 1993); blue king crabs, *Paralithodes platypus* Brandt, 1850, from the Pribilof Islands (Somerton and MacIntosh, 1985); blue king crabs from the western Bering Sea (Sasakawa, 1975); and snow crab, *Chionoecetes opilio* (Fabricius, 1788), from the northwest Gulf of Saint Lawrence (Sainte-Marie, 1993).

The results of this study are in contrast to a study conducted on Dungeness crabs in central and northern California, where gonad development began immediately after egg extrusion while the crabs were brooding eggs (Wild, 1983). This was not found in our study with Alaskan crabs. Alaskan females did not begin developing gonads until after eggs hatched in May (Fig. 2b). Wild (1983) suggested that if gonad development does not begin until after eggs hatch there will be significant differences in ovary development, which is what occurs in Dungeness crabs from southeastern Alaska. In California, all

female Dungeness crabs held in the laboratory extruded eggs (Wild, 1980) and were able to reproduce annually (Wild, 1983).

Seasonal gonad development of male crustaceans has not been widely studied. Some male crustaceans seem to have seasonal spermatogenesis activity and others appear to have continuous activity throughout the year (Sastry, 1983). The GSI of laboratory-reared male Dungeness crabs increased throughout this study (Fig. 2a). Although changes in GSI were less than 0.15%, a near doubling of gonad mass was observed (Fig. 2a). Male gonads attained maximum biomass in July.

The significant decrease in GSI from September to October 1998 among nonovigerous females in 1997 was unexpected (Fig. 2b). The decrease could be caused by one of two factors: resorption of gonads or an increase in body weight. Dry gonad weight would be expected to remain equal or increase in October, such as in the previous months. Comparisons in gonad and body weights between September and October suggest that gonads were indeed resorbed and that the decrease in GSI was not the result of increased body weight.

Resorption of gonads has not been documented in Dungeness crabs. The resorption of gonads suggested in this study occurred in the laboratory and for crabs *in situ* between September and October (Fig. 2b). If the females are not able to fertilize eggs either by mating or utilizing stored sperm, then gonads may be resorbed until the next year. In the future, a closer examination of Dungeness crab gonads, such as a histological approach, may detect resorption of individual oocytes.

Only mature crabs were assumed to be used in this study, but it should be noted that sexual maturity of crabs was not specifically determined for the crabs utilized. The differences in gonad development in this study may have resulted if nonovigerous females in 1997 were in fact immature and ovigerous females in 1997 were mature. We believe that this is highly unlikely because many researchers provide evidence suggesting that female Dungeness crabs mature at approximately 93-through 100-mm CW (Butler, 1960; Orensanz and Gallucci, 1988; Swiney, 1999) and only females 106-mm CW and larger were used in this study. Furthermore, if the nonovigerous females in 1997 were immature, then they should not be able to extrude eggs without molting and mating, but many crabs among

this group did extrude eggs in 1998 without molting and mating.

Managers should take into account our findings that all mature female Dungeness crabs are not extruding eggs annually in southeastern Alaska. Fewer animals may be produced annually than was previously thought, and management agencies should consider this in decisions. A closer examination of Dungeness crab reproductive cycles at the northern limit of their range is necessary for better management.

ACKNOWLEDGEMENTS

We thank Glacier Bay National Park and Preserve and the United States Geological Survey, Biological Resources Division, for funding this project and National Marine Fisheries Service, Auke Bay Laboratory, for the use of facilities. We thank the following for assistance with crab collections: J. deLabruere, C. O'Clair, B. Stone, T. Sands, S. Snyder, C. Lunsford, and C. Rooper. We are very appreciative to J. Mooney, J. Boldt, and D. Hess for their laboratory and field assistance and C. Armistead for GIS and map work. We thank Dr. L. Halderson, Dr. M. Adkison, R. MacIntosh, and the three anonymous reviewers for editorial and statistical advice. We especially thank Dr. S. J. Taggart for logistical, statistical and editorial support.

LITERATURE CITED

- Butler, T. H. 1960. Maturity and breeding of the Pacific edible crab, *Cancer magister*, Dana.—Journal of the Fisheries Research Board of Canada 17: 641–646.
- Fukui, Y. 1993. Timing of copulation in the molting and reproductive cycles in a grapsid crab, *Gaetice depressus* (Crustacea: Brachyura).—Marine Biology 117: 221–226.
- Grant, A., and P. A. Tyler. 1983a. The analysis of data in studies of invertebrate reproduction. I. Introduction and statistical analysis of gonad indices and maturity indices.—International Journal of Invertebrate Reproduction 6: 259–269.
- , and ———. 1983b. The analysis of data in studies of invertebrate reproduction. II. The analysis of oocyte size/frequency data, and comparison of different types of data.—International Journal of Invertebrate Reproduction 6: 271–283.
- Hankin, D. G., N. Diamond, M. S. Mohr, and J. Ianelli. 1989. Growth and reproductive dynamics of adult female Dungeness crabs (*Cancer magister*) in northern California.—Journal du Conseil International Pour l'Exploration de la Mer 46: 94–108.
- Jaffe, L. A., C. F. Nyblade, R. B. Forward, and S. D. Sulkin. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura. Pp. 451–465 in M. F. Strathmann, ed. Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast. Data and Methods for the Study of Eggs, Embryos and Larvae. University of Washington Press, Seattle, Washington.
- Jensen, G. C. 1995. Pacific Coast Crabs and Shrimps. Sea Challengers, Monterey, California. 87 pp.
- Jensen, P. C., J. M. Orensanz, and D. A. Armstrong. 1996. Structure of the female reproductive tract in the Dungeness crab (*Cancer magister*) and implications for the mating system.—Biological Bulletin 190: 336–349.

- Kobayashi, S., and S. Matsuura. 1995. Maturation and oviposition in the Japanese Mitten Crab *Eriocheir japonicus* (De Haan) in relation to their downstream migration.—*Fisheries Science* 61: 766–775.
- Lovrich, G. A., and J. H. Vinuesa. 1993. Reproduction biology of the false southern king crab (*Paralomis granulosa*, Lithodidae) in the Beagle Channel, Argentina.—*Fishery Bulletin* 91: 664–675.
- Optimas. 1993. BioScan OPTIMAS. BioScan, Inc., Bothell, Washington, U.S.A.
- Orensanz, J. M., and V. F. Gallucci. 1988. Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda: Brachyura: Cancridae).—*Journal of Crustacean Biology* 8: 187–220.
- Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Saint Lawrence.—*Canadian Journal of Fisheries and Aquatic Science* 50: 2147–2156.
- Sasakawa, Y. 1975. Studies on blue king crab resources in the Western Bering Sea-II Verification of spawning cycle and growth by tagging experiments.—*Bulletin of the Japanese Society of Scientific Fisheries* 41: 937–940.
- Sastry, A. N. 1983. Reproduction. Pp. 184–270 in D. E. Bliss, ed. *The Biology of Crustacea*. Vol. 8. Environmental Adaptations. Academic Press, New York, New York.
- Schultz, D. A., and T. C. Shirley. 1997. Feeding, foraging and starvation capability of ovigerous Dungeness crabs in laboratory conditions.—*Crustacean Research* 26: 26–37.
- Shirley, S. M., T. C. Shirley, and S. D. Rice. 1987. Latitudinal variation in the Dungeness crab, *Cancer magister*, zoeal morphology explained by incubation temperature.—*Marine Biology* 95: 371–376.
- Snow, C. D., and J. R. Neilsen. 1966. Premating and mating behavior of the Dungeness crab (*Cancer magister* Dana).—*Journal of Fisheries Research Board of Canada* 23: 1319–1323.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry—The Principles and Practice of Statistics in Biological Research*. W. H. Freeman and Company, New York.
- Somerton, D. A., and R. A. MacIntosh. 1985. Reproductive biology of the female blue king crab *Paralithodes platypus* near the Pribilof Islands, Alaska.—*Journal of Crustacean Biology* 5: 365–376.
- StatView. 1996. StatView for Windows. Abacus Concepts, Inc. SAS Institute, Cary, North Carolina.
- Swiney, K. M. 1999. Reproductive cycles of the Dungeness crab, *Cancer magister*, in southeastern Alaska.—Master's thesis, University of Alaska, Fairbanks, Alaska.
- SYSTAT. 1998. SYSTAT, SPSS, Inc. Chicago, Illinois.
- Wainwright, T. C., and D. A. Armstrong. 1993. Growth patterns in the Dungeness crab (*Cancer magister* Dana): synthesis of data and comparison of models.—*Journal of Crustacean Biology* 13: 36–50.
- West, G. 1990. Methods of assessing ovarian development in fishes: a review.—*Australian Journal of Marine and Freshwater Resources* 41: 199–222.
- Wild, P. W. 1980. Effects of seawater temperature on spawning, egg development, hatching success, and population fluctuations of the Dungeness crab, *Cancer magister*.—California Cooperative Fisheries Investigations Report 21: 115–120.
- . 1983. Comparisons of ovary development in Dungeness crabs, *Cancer magister*, in central and northern California.—State of California, The Resources Agency, Department of Fish and Game. Fish Bulletin 172: 189–196.

RECEIVED: 31 August 2000.

ACCEPTED: 16 April 2001.