GROWTH OF THE IMMATURE KING CRAB *PARALITHODES CAMTSCHATICA* (TILESIUS)

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ABSTRACT

An estimate of growth of the immature king crab of the southeastern Bering Sea is presented. From a combination of the progression of modes in successive length-frequency distributions and observations on molting, an attempt is made to identify age groups and determine age-size relationships. The growth curve derived is similar for the sexes through the first four years of life. Thereafter, female crabs grow more slowly than males and complete the immature phase in slightly less than six years. Male crabs attain sexual maturity in five years.

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INTRODUCTION

On the western coast of North America the common name " king crab " refers to anomuran crustaceans of the genus *Paralithodes.* Of the five known species of *Paralithodes* only three, *P. platypus* Brandt, *P. brevipes* Milne-Edwards and Lucas, and *P. camtschatica* (Tilesius), are of commercial importance[1]. The commercial species are benthonic animals inhabiting the continental shelves of the North Pacific Ocean and adjacent seas. Their distribution extends from the shores of eastern Korea northward to the Bering Strait and then south along the North American coast as far as British Columbia (Vinogradov, 1947). *P. platypus* is widely dispersed, but is most often encountered in the more northern regions. *P. brevipes,* the smallest species, is generally confined to localized areas in Asian waters. The third species, *P. camtschatica,* is most abundant south of 58° North latitude, and is the principal contributor to the king crab fisheries in both Asia and North America. This report is restricted to biological observations on *P. camtschatica.*

Exploitation of king crabs began in northern Japan and southeastern Siberia shortly before the turn of the century. The initial king crab industry was a shore-based operation, but around 1920 factoryships were developed which led to eventual expansion of this fishery into North American waters. The Japanese began to use factoryships in the southeastern Bering Sea in 1930, but this operation was discontinued in 1939. The king crab stock remained untouched until 1947 when the United States established a king crab fishery in the southeastern Bering Sea. The United States exploited these stocks alone until 1953 when the Japanese resumed a factoryship operation. Re-establishment of the Japanese fishery caused concern that the combined catch of the Japanese and United States operations might exceed the level of maximum sustained yield of the stock. Thus, in 1954 the United States undertook a joint study with Japan to determine the need for conservation measures for the king crab stock of the southeastern Bering Sea. As a part

[1] The other two species, *P. rathbuni* (Benedict) and *P. californiensis* (Benedict), have been collected infrequently in deep water off the coast of California.

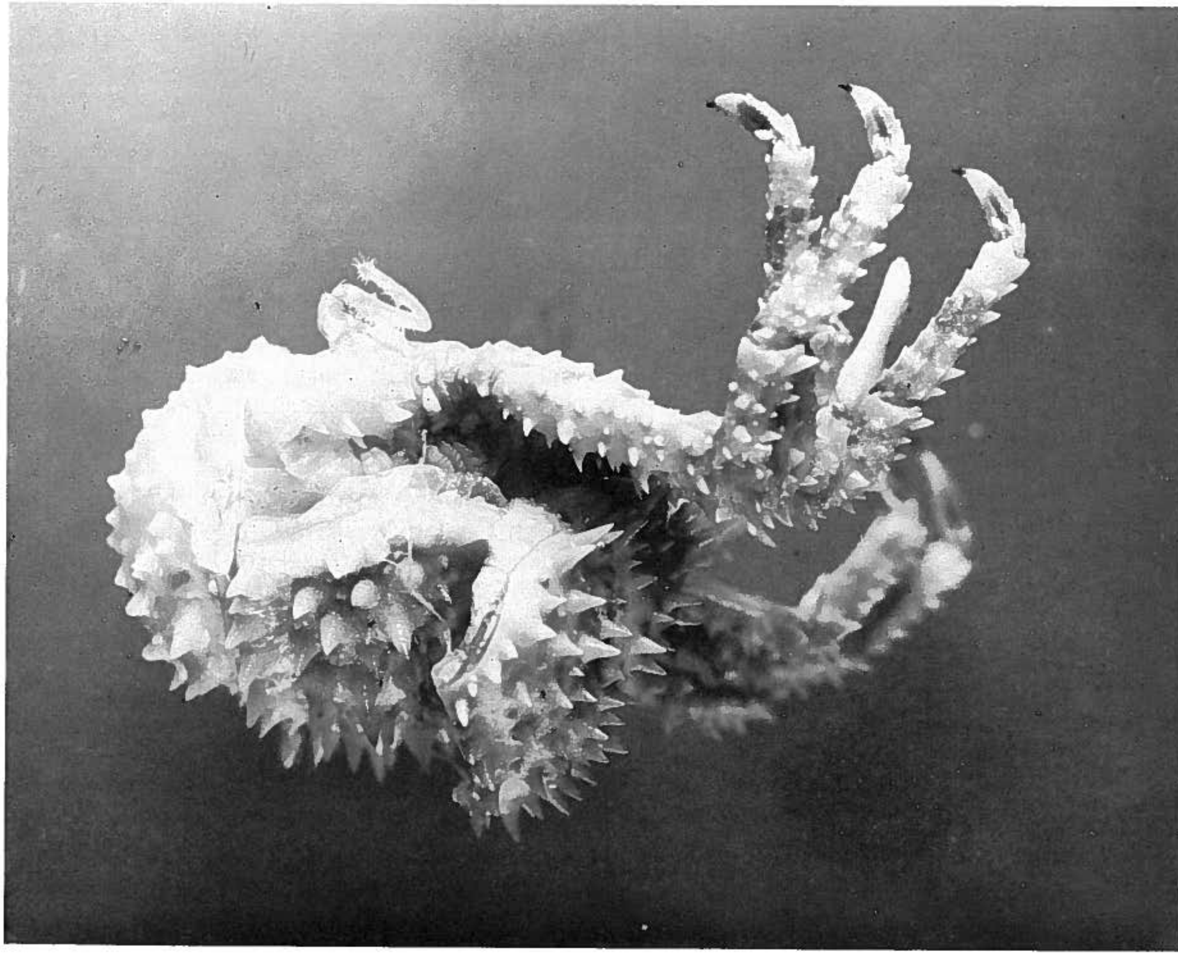

FIGURE 1. Molting immature king crab. The crab is withdrawing itself from the old shell, part of which is seen in the lower center.

of this general program to assess the need for conservation measures, the U.S. Fish and Wildlife Service initiated a study in 1958 to investigate the growth of immature king crabs.

The objectives of this report are to describe molting of immature king crabs of the southeastern Bering Sea, the changes in length and weight which accompany molting, and the resultant rate of growth. Figure 1 is a photograph of a molting immature king crab; it is included in order that the reader may gain some feeling and insight of this unusual manner of growth.

PREVIOUS GROWTH STUDIES

Published estimates of growth of immature king crabs indicate variation in growth not only between geographic areas but also within the same general locality. Examples of this variability are shown in Figure 2. The curves represent growth for both male and female crabs, and include only immature animals. The growth curves derived from reports by Wang (1937), Nakazawa (1912), Kurata (1961 b), and Marukawa (1933) are for Asiatic crabs; those presented by Powell (1960 a) and Bright *et al.* (1960) are for Gulf of Alaska king crabs. Although it is recognized that growth rates undoubtedly vary as a result of environmental and racial differences, the dissimilarities in the growth curves appear to be greater than can be ascribed entirely to these sources.

Marukawa's (1933) growth curve was derived from modes observed in width-frequency data; each mode was considered an age group. Mackay and Weymouth (1935), Kurata (1961 b), and Sato (1958) point out that several of the modes considered by Marukawa as age groups are probably instars. If these modes were deleted, Marukawa's growth curve would agree well with that of Kurata presented in Figure 2. Bright *et al.* (1960) formulated a growth curve for immature king crabs of Cook Inlet based on growth per molt and frequency of molt of crabs

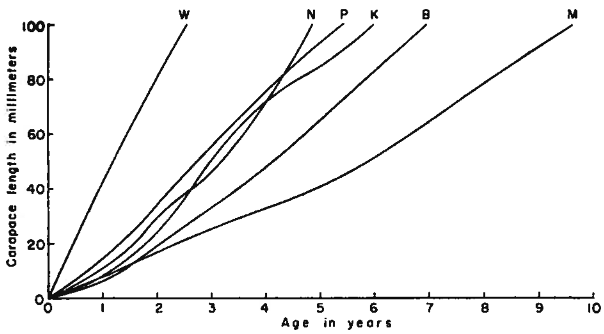

FIGURE 2. Growth curves for immature king crabs. Curves derived from Wang " W " (1937), Nakazawa " N " (1912), Kurata " K " (1961b), and Marukawa " M " (1933) are for Hokkaido king crabs. Those by Powell " P " (1960a) and Bright *et al.* " B " (1960) are for Gulf of Alaska crabs. Results by Marukawa, Wang and Nakazawa were originally expressed in terms of carapace width, but are shown here by carapace length. The conversion from width to length was made on the basis of data presented in Tables 4 and 5.

retained in live boxes. Some question always exists concerning the effect confinement may have on the frequency of molting and growth per molt. Unfortunately, Bright *et al.* did not present data by which this effect may be evaluated. Powell's (1960 a) age-length curve for immature king crabs of the Kodiak area was derived from modes in successive length-frequency distributions and growth per molt as observed from tagged crabs. As mentioned by Powell this estimate of growth is tentative because various portions of the growth curve were based on limited data. Wang (1937) estimated growth of immature king crabs from width-frequency distributions taken in 1925 and 1926 off the Kitami coast of Hokkaido. These data showed modes at carapace widths of 45 and 85 mm which Wang interpreted as age groups representing the first and second years of life. There was a semblance of a third mode at 115 mm but Wang did not consider it as an age group; he chose instead the next larger mode at 135 mm as the average size of crabs three years after hatching. Nakazawa (1912) estimated growth of Hokkaido crabs by combining data from his studies of king crab with published information on the frequency of molt and growth rate of *Homarus americanus* and *Cancer pagurus*. The growth curve for Hokkaido crabs by Kurata (1961 b) is based on growth per molt, and frequency of molt in relation to environmental temperature. As expressed by Kurata the amount of growth per molt was obtained from confined crabs, and other data utilized are fragmentary; thus the growth curve is only an approximation. Other investigators have studied size-frequency distributions (Kajita and Nakagawa, 1932) and growth per molt (Takeuchi, 1962; Sato, 1958) of immature king crabs, but the data in their reports are not sufficient to permit construction of growth curves.

MATERIALS AND METHODS

SELECTION OF SAMPLING AREA

The small size and frequent molting of immature king crabs preclude use of current methods of tagging, and there exists no known or suggested means of determining age by body structures. Thus, the only practical means of assessing growth, aside from observation of confined individuals, is to examine the progression of modes in size-frequency distributions obtained from successive samples taken in the natural environment.

The difficulty of obtaining representative samples of immature king crabs throughout their entire size range proved to be a major obstacle in determining growth by modal progression. Representative sampling of immature crabs is complicated primarily by their distribution. The larval crabs settle and tend to remain in the eulittoral zone until the carapace length reaches 40 to 50 mm. At this size the immature crabs begin to emigrate from shallow water to the sublittoral fishing grounds. As their size increases, their range of vertical movement also increases, but they are not found in quantity on the fishing grounds until they attain a length of 70 to 80 mm. Reports by Nakazawa (1912) and Takeuchi (1960), as well as surveys by the U.S. Fish and Wildlife Service, suggest that although immature crabs shorter than 60 mm are present in deeper water where fishing is conducted their distribution is not uniform either in quantity or size range. Also, the king crab is a gregarious animal, especially in early life, and solitary individuals are rarely encountered. Most immature crabs are found in groups called pods which may be composed of several hundred to several thousand individuals of similar size (Bright *et al.*, 1960; Durham, 1958; Powell, 1960 b). The shape of a pod resembles a haystack. Periodically, individuals of a pod disperse for feeding and later reassemble, often in the original location. This clustered distribution makes blind sampling with nets or trawls difficult, since most attempts will miss the crabs completely.

In May 1957, the U.S. Fish and Wildlife Service devoted 10 days to sampling the eulittoral zone along the north shore of the Alaska Peninsula. Only 85 immature king crabs were taken during this survey—77 of them in one beam trawl haul. In this same year a single beach seine haul in Akutan Bay in the Fox Islands took over 200 immature crabs. Another seine haul in shallow water near Unalaska Island in the

Aleutian chain provided an additional 30 immature crabs. Because of the difficulty of obtaining sufficient samples from a vessel, or maintaining a shore station on the coast adjacent to the Bristol Bay fishery, it appeared that if adequate samples of immature crabs were to be collected it would be advantageous to undertake sampling from a shore-based station on one of the populated Aleutian Islands. It was recognized that crabs from the Aleutian Islands might be of a different population and subject to an environment somewhat dissimilar to that of the Bristol Bay region; still the facilities available on a populated Aleutian Island would allow periodic sampling of immature crabs throughout the year. From successive samples collected, especially samples of smaller immature crabs (2 mm to 60 mm carapace length) which inhabit the eulittoral zone, a basic estimate of growth of immature crabs could be made. As information was accumulated from annual sampling of larger immature crabs (60 mm carapace length and greater) taken on the Bristol Bay commercial fishing grounds, it was to be interpreted in terms of this basic growth estimate. Therefore, in 1958 the U.S. Fish and Wildlife Service initiated a program to assess the growth of immature king crabs inhabiting the shallow waters of Iliuliuk Bay near Unalaska, Alaska.

The Bristol Bay region is geographically defined as the area north of the Alaska Peninsula and east of Unimak Pass. The king crab fishery of this area is located in the southern half of Bristol Bay. As used in this report, " Unalaska " includes only Iliuliuk Bay and vicinity; however, these observations are probably applicable to any area on the north side of the Fox Island group. Also, " southeastern Bering Sea " includes only the continental shelf bordering the northeast coast of the Fox Islands and the southern half of Bristol Bay.

Sampling Procedures

In the summers of 1955 through 1961 the U.S. Fish and Wildlife Service conducted an offshore survey of king crabs inhabiting the Bristol Bay fishing region. Samples were collected by otter trawls fished at predesignated stations 20 miles apart. At each station all crabs caught were measured, shell condition and sex were noted, and males were tagged and released. Sampling in the Bristol Bay region was described by Weber and Miyahara (1962). The remainder of this subsection pertains to sampling at Unalaska, but methods of measurement and designations of molting stages discussed are equally applicable to samples of immature crabs from the Bristol Bay fishing region.

Sampling of immature king crabs at Unalaska was carried out during four intervals from April 1958 through May 1959. Areas in which samples were

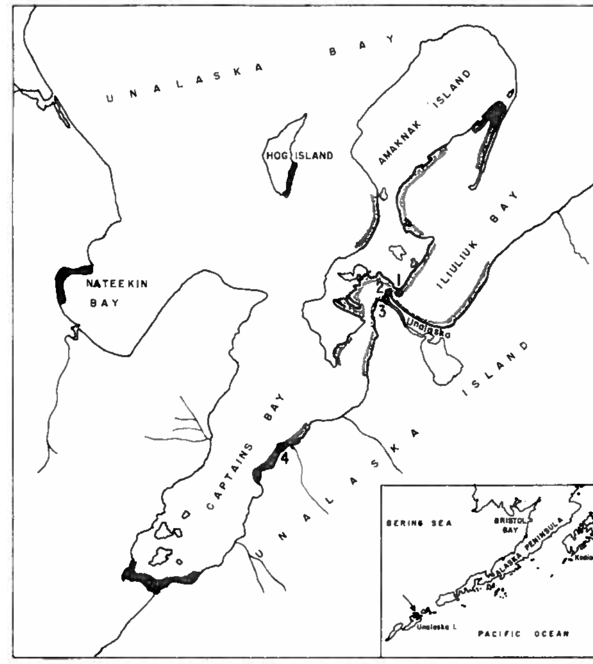

Figure 3. Area of king crab study at Unalaska. Shading indicates regions surveyed for presence of immature king crabs during each sampling period. Numbers indicate locations where the majority of immature crabs were collected.

collected are shown in Figure 3. Dates of sampling were as follows: (1) first period from April 22 to June 6, 1958; (2) second period from September 17 to October 1, 1958; (3) third period from February 11 to February 24, 1959; (4) fourth period from May 24 to June 2, 1959.

The most successful method of obtaining immature king crabs at Unalaska was by SCUBA diving. Other methods of capture, such as $2\frac{1}{4}$-inch (stretched mesh) tangle nets, shrimp pots, ring nets, and stomach samples of predators, yielded less than one percent of the crabs collected. During each sampling period spot checks were made at depths down to 30 feet throughout the areas indicated in Figure 3. In areas where immature crabs were found, repeated collections were made at intervals of several days, and adjacent localities were carefully surveyed.

Upon capture, king crabs were placed in holding cages until the end of the sampling period to prevent repeated captures and to observe molting. In an attempt to maintain natural conditions the cages were suspended beneath the Unalaska pier (sampling area 2 in Fig. 3)—an area found to be continuously inhabited by immature king crabs. The cages were raised daily to feed the crabs and to measure those which had molted. A supply of mussels, barnacles, and fresh fish was maintained in the holding cages.

Sex was recorded for each king crab at time of collection (females are distinguished by the asymmetrical distribution of abdominal plates and presence of abdominal pleopods).

Measurements Taken

Linear measurements used in this study are length and width of the carapace measured to the nearest millimeter with vernier calipers. Carapace length (Fig. 4) is defined as the distance of a slanted line ex-

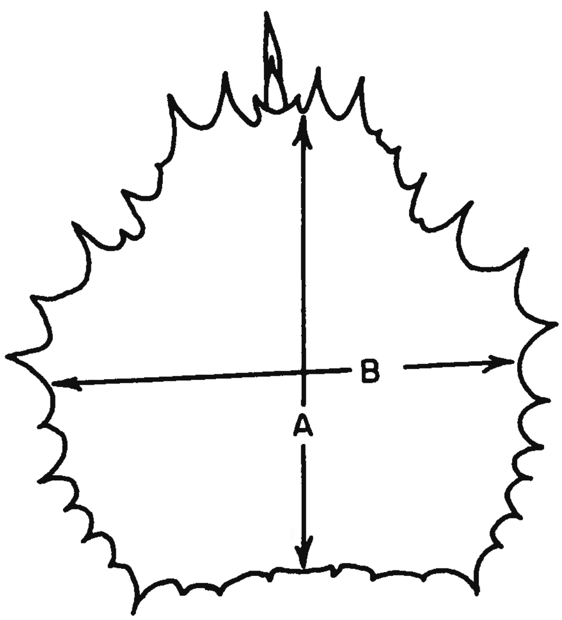

Figure 4. Outline of king crab carapace showing dimensions measured. A=length; B=width.

tending from the posterior median edge of the carapace to the extreme concavity of the right eye orbit; carapace width is taken as the greatest width of the carapace between marginal spines. Carapace length was recorded for each crab collected. Carapace width was recorded for all crabs collected in the first week of sampling of the first and third periods. (For immature crabs sampled in the Bristol Bay fishing region carapace width was recorded in 1957 and 1961.)

Weight was measured to the nearest gram. Prior to weighing, crabs were drained for 10 minutes to remove excess water. Crabs weighing less than 1 g were grouped by millimeter length class, weighed as a unit, and the average individual weight calculated.

Shell Condition and Molting Stages

Because king crabs grow by a series of steplike increments, a crab of one size group may suddenly advance into a larger size group. Thus, the presence of two closely adjacent modes in a length-frequency distribution raises the question of whether they represent two unrelated groups or only a single group in the process of molting. The distinction between molting and non-molting crabs may be made on the basis of differences exhibited at each stage in the molting cycle.

Methods of identifying various phases of the molting cycle have been developed for some brachyuran crabs (Hiatt, 1948; Drach, 1939; Passano, 1960). These methods are based on sclerotization rates (shell hardening), physiological differences, and changes in the newly developing integument. Because we are concerned primarily with differences between groups which are and are not actively molting, an easily discernible criterion such as sclerosis is applicable. In the first sampling period king crabs were classified by carapace hardness. This character is a subjective measurement based on the degree of carapace flexibility, and is determined by application of slight manual pressure on the sides of the carapace. From observations on progressive carapace hardening of newly molted immature crabs it was found that this classification (i.e., either rigid or flexible) could be used to distinguish individuals which had molted within approximately two days prior to collection.

Color changes also have been observed prior to molting. Bright *et al.* (1960), Powell (1960 c), and Sakuda (1958) have observed a darkening of noncalcified joint areas prior to molting in both immature and adult female king crabs. These differences are evidently associated with the molting process and have also been observed in premolting brachyuran crabs (Guyselman, 1953; Drach, 1939). During the initial sampling period at Unalaska, conspicuous differences in coloration of the exoskeleton were noted, and in subsequent sampling periods coloration combined with shell hardness provided a means of classifying crabs into molting stages suitable for this study.

The molting stages used as the basis of classification in this report are as follows:

Stage 1. *Postmolt:* A period immediately following molting; weight stabilizes and linear increase terminates. Carapace is bright red and integument is flexible for one to two days after molting.

Stage 2. *Intermolt:* State of stable linear dimensions, initiated when the integument becomes rigid. During this, the lengthiest, stage of the molting cycle carapace coloration changes from a bright red to a dull red-brown. White ventral surfaces of the exoskeleton become progressively scratched and yellow as the intermolt stage progresses.

Stage 3. *Premolt:* A period of preparation for molting. The non-calcified joints of the appendages become dark red and the exoskeleton usually takes on a dark brown appearance. Terminal phases of this stage include abdominal swelling and sloughing of abdominal plates immediately prior to molting.

Stage 4. *Molt:* Actual casting of the exoskeleton accompanied by initial linear expansion and weight increase[2].

Observations on Molting

Throughout the year of study at Unalaska, molting of 317 king crabs was observed. The basic data are given in Appendix Table I. Twelve crabs had molted shortly before collection (their cast shells were found adjacent to them). The remaining observations were taken from crabs which molted in confinement.

The limited facilities at Unalaska prevented separation of confined king crabs into small groups. Thus, between daily checks, often 10 or more crabs of similar size molted in the same holding cage. To determine the individual growth increment in this situation it was necessary to identify each cast carapace correctly with the respective postmolt crab. Tagging or marking was undesirable since the effect on growth is not known. Therefore, individual differences were investigated to find means of identifying the cast shell with its former owner.

Urita (1931) studied the number and arrangement of spines on the carapace of Karafuto (southern Sakhalin) king crabs with the objective of identifying king crab stocks. He did not find a significant variation between stocks by this method, but he did find a fairly uniform arrangement of major spines and a great variation in arrangement of minor spines. The Unalaska study indicated that variation in spine arrangement may be used to identify individual immature crabs. From our observations it appears that the arrangement of minor spines, although it becomes less obvious in larger crabs, is an individual characteristic persisting throughout life. In all comparisons made, no two spine arrangements were identical. Through identification by spines, the growth increment per molt was determined for each individual by matching the cast carapace with the newly molted crab. Measurements made on the exuviae were identical with measurements made on crabs prior to molting.

[2] Although no study was made of the changes in the integument, Stage 1 above is generally comparable to Stages A and B described by Drach (1939) and Hiatt (1948) for brachyuran crabs, and Stages 2 and 3 are similar to their C and D stages. For intermolt stages of brachyurans as cited by Passano (1960), Stage 1 above corresponds to Stages A and B, and Stages 2, 3, and 4 are Stages C, D, and E, respectively.

GROWTH DESCRIPTION AND ANALYSIS

The following sections are a description and analysis of information derived from observations of immature king crabs in the Bristol Bay fishing region and at Unalaska. The first section treats the development and growth of the embryonic and larval crab. The most comprehensive data on egg and larval development are from Japanese investigations conducted in Bristol Bay. Duration of larval development at Unalaska is based primarily on Japanese findings. The second and third sections discuss allometric changes in the carapace with size, and growth per molt in terms of linear expansion and increase in weight. These data provide background for the analysis of advancement of modes since the observed progression of modal lengths in successive length-frequency distributions reflects changes which take place at molting. The fourth section concerns growth of immature crabs through the first three years of life. Data for this phase are from studies at Unalaska in 1958 and 1959. The fifth section presents the results of annual sampling of immature crabs by the U.S. Fish and Wildlife Service in Bristol Bay from 1957 through 1961. From these observations the growth of immature crabs from an age of four years through maturity was estimated. In the final section data on the growth of immature crabs obtained from Unalaska and Bristol Bay are combined to give a growth curve for immature crabs of the southeastern Bering Sea.

Development and Growth of Embryonic and Larval King Crabs

Embryo Development and Time of Hatching

Mature male and female king crabs undertake a characteristic annual migration pattern which appears to be similar throughout their distribution (Vinogradov, 1945; Bright *et al.*, 1960; Marukawa, 1933). Migration is in two principal stages: inshore to shallow water during the spring; offshore to deeper water at the start of summer. Inshore movement has been termed spawning migration. It generally starts in February and March, reaches a peak in April, and is completed by May. Developing eggs, which the female has been carrying for almost a year, hatch during spawning migration. The female then molts, mates, and ovulates usually within a 1–2 day interval. Studies by the Fisheries Agency of Japan (1963 a) indicate that a female crab must mate within one week after molting if ovulation and fertilization are to be successful.

Egg development has been studied and described in detail by Kajita and Nakagawa (1932) and Marukawa (1933). Briefly, the fertilized egg undergoes superficial cleavage and attains the gastrula stage 20 to 25 days after fertilization. Within 60 days the embryo enters the nauplius stage. Five months after fertilization, pre-zoeal characteristics appear. This form is retained until shortly after hatching.

Time of hatching is important since it represents the base point from which age is calculated. Vinogradov (1941) found that hatching of king crab eggs takes place in March off the west coast of Kamchatka and in April in the Bay of Peter the Great. In the Nemuro region, Marukawa (1933) observed hatching from the middle of March to the beginning of May, with a peak around April 20. Nakazawa (1912) mentioned that crabs inhabiting waters adjacent to the Nemuro region hatch mainly in April, and by May 10 over 70 percent of the females carry empty egg cases.

Time of hatching in Bristol Bay may be estimated from data by Takeuchi (1962) for 1960. The Fisheries Agency of Japan (1963 a) and Niwa (1962) have made estimates for 1961 and 1962, respectively. These estimates are based on the timing of reproductive activities determined from observed changes in the condition of eggs carried by the female. Occurrence of females bearing eyed eggs, residual egg membranes, and new eggs in 1960, 1961, and 1962 are shown in Figure 5. Time of hatching extends from mid-April to mid-June; 50 percent hatching falls in mid-May. These data are consistent with similar observations by the Fisheries Agency of Japan (1956) in 1954. In 1955 and 1963 (Fisheries Agency of Japan, 1956 and 1963 b), 50 percent of the eggs hatched two to three weeks earlier.

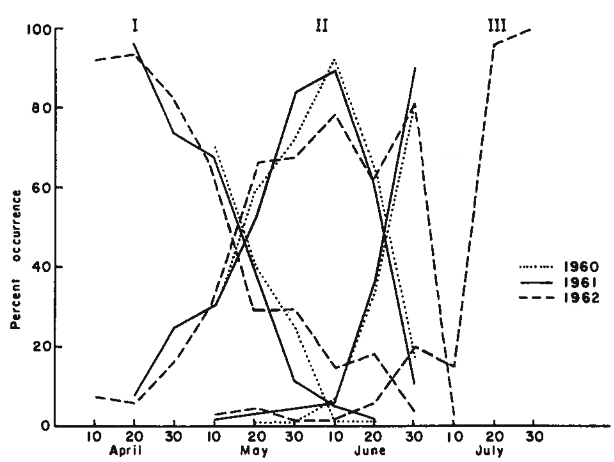

FIGURE 5. Percent occurrence, by 10-day intervals, of female king crabs bearing eyed eggs (I), empty egg cases (II), or new eggs (III) in 1960 (data from Takeuchi, 1962), 1961 (data from Fisheries Agency of Japan, 1963a), and 1962 (data from Niwa, 1962).

Time of hatching of king crabs in the vicinity of Unalaska was estimated from observations of the abundance of cast adult female shells, type of eggs carried by adult females, and time of mating activity as observed by Unalaska residents. The combined observations indicate that the peak of hatching in the Unalaska area probably occurs around mid-April. This date is several weeks earlier than in the Bristol Bay region, but the difference is not surprising if water temperature influences reproductive behavior. Sato (1958), who compiled all available data on the time of king crab spawning in Asian waters, noted a delay of one month in the spawning of northern Kuril Island crabs over crabs from the more southerly Nemuro area. As mentioned by Sato, the differences in spawning times are probably caused by differences in inshore water temperatures, which in turn might cause the period of reproductive activity to vary from one area to another and, within the same geographical area, from year to year. As will be shown in the following section, water temperatures at Unalaska are several degrees warmer than in Bristol Bay.

Larval Growth

Upon hatching the pre-zoeal larvae molt, usually within minutes, into the zoeal form. The basic zoeal structure is maintained for three consecutive molts, and on completion of the fifth molt the king crab changes into the glaucothoe larvae. The adult form is reached after the sixth molt. Morphological changes from molt to molt during larval life were described in detail by Marukawa (1933), Kajita and Nakagawa (1932), Sato and Tanaka (1949 a), and Sato (1958). Studies by Kurata (1959, 1960 a, 1960 b) and Sato and Tanaka (1949 b) considered the effect of temperature, salinity, and food supplies on growth and duration of each larval stage.

The vertical distribution of king crab larvae depends upon their developmental stage. First-stage zoeae are generally in the middle and upper water layers and as they pass through successive stages they sink to lower layers to become bottom dwellers as glaucothoe larvae. There is evidence of some diurnal vertical movement (Takeuchi, 1960), but this movement does not obscure the general downward shift as zoeae undergo successive molts.

Kurata's (1959, 1960 a, 1960 b) studies on larval and post-larval development of the king crab indicate that when adequate food is available the most important factor influencing growth is temperature. Data from Kurata (1960 a, 1961 a) show that a decrease of temperature from 10°C to 5°C doubles the length of larval life. Thus, to approximate the time at which the first adult form appears it is necessary to consider the temperature of the water which the larvae inhabit. The temperature of inshore waters of the southeastern Bering Sea during the winter is characteristically uniform from surface to bottom (U.S. Navy Hydrographic Office, 1958). In early spring a minor thermocline is usually present in the upper 10 meters. This thermocline descends rapidly, and by the end of July the surface and bottom temperatures are again nearly identical but are considerably warmer than in the winter. Isothermal conditions usually prevail throughout August and September (Dodimead *et al.*, 1963).

Since all zoeal stages, except perhaps the first when the water is essentially isothermal, are intimately associated with the middle and lower water layers, an average of bottom water temperatures should provide a reasonable indication of the temperature environment of king crab larvae. According to studies of current flow by Hebard (1959) and observations by Takeuchi (1962), bottom temperatures off Black Hill and Port Moller should be most representative of temperatures encountered by king crab larvae of the Bristol Bay region. The average inshore water temperatures at the bottom for this area of the southeastern Bering Sea for 1955 through 1961 are given in Table 1. The year-to-year variation in water temperature within this area is striking. Temperatures below 0°C were recorded in the spring of 1956 and 1959. In contrast, high bottom water temperatures of 10°C and 11°C, as recorded in August of 1938 (Favorite and Pedersen, 1959), 1939, and 1940 (Dodimead *et al.*, 1963), were uncommon during these seven years of study.

TABLE 1. Average bottom water temperatures by month off Black Hill and Port Moller, Alaska, for 1955 through 1961. Data from observations by the U.S. Fish and Wildlife Service at depths of 15 to 25 fms.

Month	Average bottom temperature (°C)	Range (°C)
May	2.1	−0.3 to 3.7
June	3.9	1.2 to 5.1
July	6.0	3.1 to 9.6
August	7.3	3.9 to 10.7

Aside from limited work by Shimizu (1936), experiments on the relation between growth of king crab larvae and water temperature have been conducted only at temperatures above 4°C. Kurata (1960 b, 1961 a) has demonstrated, however, a generally linear relationship between temperature and time required for development which may be expressed in degree days (degree days = cumulative average daily temperatures expressed in degrees centigrade). Development from hatching to the young adult form requires approximately 460 degree days (Kurata, 1961 b). On the basis of information from Kurata's estimate, a pre-zoea hatched in the Bristol Bay region in early May would attain the young adult form by mid-August.

In his 1960 study of diurnal migration of king crab zoeae in the southeastern Bering Sea, Takeuchi (1962) investigated the time of greatest abundance of each zoeal stage. In mid-May most zoeae collected were in the first stage, but a few second-stage individuals were also present. Second-stage zoeae are abundant from the end of May to mid-June. Although catches decreased to insignificant numbers by mid-June, it appeared that the majority of the second-stage zoeae were transforming into third-stage zoeae. Comparing his data with those of Marukawa (1933), Takeuchi concluded that it would take nearly one more month for the zoeae to reach the peak of the fourth stage, and an additional two weeks before a majority attained the glaucothoe stage in late July. According to Marukawa (1933) the majority of glaucothoe would metamorphose into the adult form two weeks later, or by the middle of August. This view is in agreement with the above estimate of duration of the larval stage as calculated in degree days.

Attempts to sample king crab zoeae at Unalaska were unsuccessful. Several glaucothoe larvae were collected in mid-June of 1958, but they did not appear to be numerous. The best available means of determining when the first adult form would probably appear in Unalaska waters would be by applying Kurata's (1961 b) estimate of degree days to the water temperature at Unalaska. The average monthly water temperatures at Unalaska for April through August are listed in Table 2. The average bottom temperature recorded at 6 fms for April and May 1958 was 0.3°C above the average shown in Table 2.

TABLE 2. Average water temperature at Unalaska for 1946 through 1951 (from U.S. Coast and Geodetic Survey, 1952; original data were in °F).

Month	Temperature (°C)
April	4.1
May	5.2
June	7.0
July	9.1
August	9.8

Since the peak of hatching occurs in mid-April at Unalaska, the first adult form should appear 460 degree days later, or in early July. This estimate is in agreement with Marukawa's (1933) observations of larval development in Nemuro waters. Time of hatching and water temperatures recorded by Marukawa are almost identical with those at Unalaska.

The water temperatures presented for Unalaska and Bristol Bay are not directly comparable. Bottom temperatures for Bristol Bay were taken at 15 to 25 fms, whereas observations at Unalaska were at depths not exceeding 10 fms. Limited hydrographic observations by personnel of the U.S. Fish and Wildlife Service in Bristol Bay indicate that at a comparable depth the difference of temperature between the two areas does not exceed 2°–3°C. Thus, the above estimates of mid-August for the Bristol Bay region and early July for Unalaska only generally approximate the time at which the first adult forms of king crab appear. Larvae hatched at the same time and inhabiting similar depths in both areas probably metamorphose into the adult form within a few weeks of each other.

Size Range of Immature King Crabs

The immature phase in the king crab extends from the time the larval crab metamorphoses into the adult form until sexual maturity. From rearing experiments, Kurata (1959, 1961 a), Sato and Tanaka (1949 a), and Bright *et al.* (1960) found the smallest adult form to have a carapace length of approximately 2 mm. It is interesting to note, however, that the size at sexual maturity varies from region to region. On the basis of the presence or absence of eggs carried by the females, Marukawa (1933) remarked that the average size of females at sexual maturity in the vicinity of Nemuro (northeast coast of Hokkaido) is 10–20 mm greater than off the coast of Kamchatka. Wallace *et al.* (1949) indicated that the size at which Bering Sea female crabs become oviferous ranges from 86 mm to 102 mm (carapace length), whereas in the Gulf of Alaska maturity is reached at lengths of 93–122 mm. Powell and Nickerson's (1965) observations on maturity of female crabs in the vicinity of Kodiak Island, Alaska, concur with the findings reported by Wallace *et al.* (1949) for female crabs of the Gulf of Alaska.

The percentage oviferous, by carapace length, of female crabs collected by the U.S. Fish and Wildlife Service in the southeastern Bering Sea from 1956 through 1958 is shown in Figure 6, which was plotted from data given in Table 3. These data agree with the results of Wallace *et al.* (1949) for female crabs from the southeastern Bering Sea in 1941. It should be noted that validity of figures on percentage oviferous depends on representative sampling for both mature and immature female crabs. The consequence of a disproportionally greater number of mature females, which is characteristic of these data as a result of sampling, tends to shift the oviferous ogives in Figure 6 slightly to the left. From the observed frequency of egg-carrying females it appears that the majority of female crabs in the southeastern Bering Sea mature at a carapace length between 90 mm and 100 mm.

Another method of detecting maturity is through changes in proportion of various body parts. It was

Table 3. Percentage of female king crabs oviferous, by carapace length, in southeastern Bering Sea, 1956–58.

	Sampling year								
	1956			1957			1958		
Carapace length (mm)	No eggs	With eggs	Percent with eggs	No eggs	With eggs	Percent with eggs	No eggs	With eggs	Percent with eggs
70 & less	3	0	0	21	0	0	75	0	0
75	5	0	0	45	1	2.2	28	2	6.7
80	11	2	15.4	86	0	0	86	7	7.5
85	7	2	22.2	76	2	2.6	189	69	26.7
90	22	7	24.1	46	26	36.1	225	196	46.6
95	12	5	29.4	36	58	61.7	82	258	75.9
100	7	33	82.5	20	156	88.6	19	351	94.9
105	3	39	92.9	8	175	95.6	4	550	99.3
110	0	18	100.0	2	153	98.7	3	726	99.6
115	0	43	100.0	3	184	98.4	3	617	99.5
120	0	30	100.0	2	249	99.2	1	505	99.8
125	1	10	90.9	0	233	100.0	0	345	100.0
130	0	14	100.0	0	150	100.0	1	298	99.7
135	0	23	100.0	0	85	100.0	1	199	99.5
140	0	12	100.0	0	60	100.0	0	128	100.0
145 & over	0	23	100.0	0	119	100.0	0	238	100.0
Total	71	261		345	1,651		717	4,489	

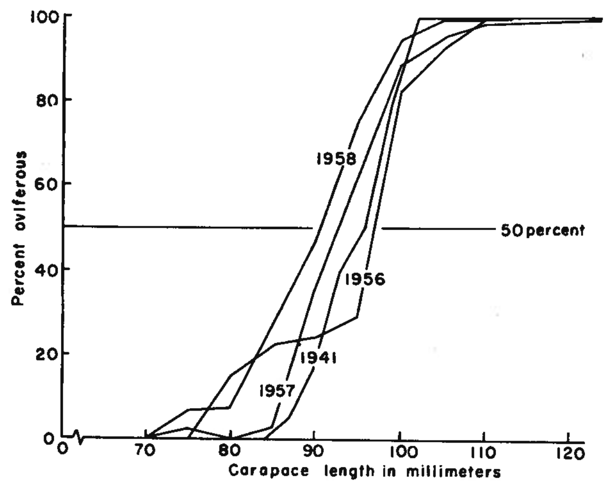

Figure 6. Percentage oviferous by carapace length of female king crabs collected in the southeastern Bering Sea in 1941, 1956, 1957, and 1958. The 1941 data are from Wallace *et al.* (1949).

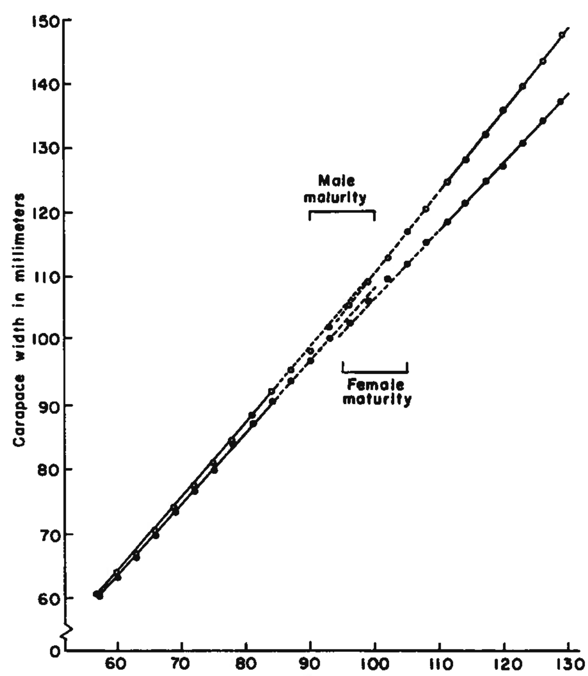

Figure 7. Length-width relationship for male and female king crabs of the southeastern Bering Sea. Open and closed circles represent average values by 3 mm length intervals for males and females, respectively. Solid lines were fitted by regression analysis; broken lines are extensions of the solid lines. Data on which this graph is based are given in Tables 4 and 5.

demonstrated by Marukawa (1933) and Wallace *et al.* (1949) that a change in carapace length relative to other morphological dimensions (carapace width, merus length, chela length and chela height) is a secondary sexual characteristic of female king crabs. The size at which allometric changes take place in females corresponds in general to the size at which they become oviferous. A comparison of the relative growth of carapace length and carapace width for king crabs from the southeastern Bering Sea is presented in Figure 7. A break in the length-width line for female crabs occurs at a length of 95 mm to 105

Table 4. Carapace length-width relationship in male and female king crabs collected in Bristol Bay in 1957 and 1961.

	Male			Female		
Carapace length (mm)	Average width by 1 mm group	Average width by 3 mm group	*N*	Average width by 1 mm group	Average width by 3 mm group	*N*
56–58		60.4	10		60.7	11
59–61		63.9	33		63.3	19
62–64		66.8	65		66.5	62
65–67		70.7	50		69.8	58
68–70		74.0	57		73.3	57
71–73		77.8	44		76.6	39
74–76		81.1	38		80.0	42
77–79		84.7	22		84.2	35
80–82		88.5	26		87.1	79
83–85		92.3	29		90.7	139
86–88		95.5	33		93.8	42
89–91		98.3	43		97.0	46
92–94		102.2	44		100.3	47
95–97		105.7	43		103.2	38
98–100		109.4	44		106.4	40
101–103		112.8	46		109.5	43
104–106		116.9	50		112.0	43
107–109		120.4	51		115.3	38
110	122.9		171	117.5		34
111	124.6	124.2	132	118.2	118.5	29
112	125.5		144	120.2		31
113	126.9		152	120.4		40
114	127.9	128.1	199	122.3	121.4	37
115	129.2		203	121.5		29
116	139.7		189	123.2		26
117	131.6	131.8	194	125.3	124.8	24
118	133.1		179	126.0		26
119	134.6		170	126.3		33
120	135.9	135.8	198	127.7	127.2	23
121	136.9		152	127.9		18
122	138.1		174	129.5		28
123	139.4	139.5	182	130.5	130.5	28
124	140.9		179	131.8		19
125	142.1		198	133.3		10
126	143.3	143.3	171	132.8	134.2	8
127	144.8		169	135.4		18
128	145.9		171	136.3		22
129	147.7	147.4	147	137.4	136.9	17
130	148.9		153	137.4		15

mm. A change in ratio of carapace length to width for males is not as evident as in females, but a slight flection appears at 90 mm to 100 mm (carapace length). Wallace *et al.* (1949) found that for male crabs of the southeastern Bering Sea a change in the relative growth of merus and chela dimensions occurred at approximately 100 mm (carapace length). Also, from histological examination of the relative degree of proliferation of cells lining the ductus deferens, Wallace *et al.* (1949) tentatively concluded that the minimum length at which males from the southeastern Bering Sea become mature is betwen 85 mm and 90 mm.

TABLE 5. Basic statistics for relation of carapace length to carapace width of male and female king crabs collected in the Bristol Bay region in 1957 and 1961.

Sex	Size range of carapace length (mm)	*N*	Slope *b*	Intercept *a*
Female	56-85	541	1.140	−5.244
Female	110-130	515	1.070	−0.437
Male	56-85	374	1.182	−7.347
Male	110-130	21[1]	1.267	−16.334

[1] Average values by 1 mm group as given in Table 4.

On the basis of the above discussion, the size range of immature king crabs in the southeastern Bering Sea is considered to extend from 2 mm (carapace length), as the first adult form, to approximately 95 mm at maturity.

GROWTH AT MOLTING

Molting Stages

Detailed descriptions of molting activity in king crabs may be found in Bright *et al.* (1960), Marukawa (1933), Takeuchi (1960), and Sakuda (1958). A brief resume of observations recorded at Unalaska is presented below. One or two weeks prior to molting, external coloration of the exoskeleton changes from a dull red to a dark brown and spaces between the abdominal plates begin to widen slightly. These changes indicate termination of the intermolt stage and initiation of the premolt stage. Approximately three days before casting of the old shell, the abdomen begins to enlarge. The rate of abdominal distention, although initially slow, increases rapidly 12 to 18 hours before molting. Sloughing of the abdominal plates occurs immediately prior to molting. These findings are in contrast to observations by Takeuchi (1960), Powell (1960 c), and personnel of the Fisheries Agency of Japan (1963 a), who reported that abdominal swelling begins only one to six hours before molting.

Twelve king crabs (29–39 mm in length) taken at Unalaska in the first sampling period were observed to be on the verge of molting and were placed in trays of sea water. Casting of the old shell required an average of nine minutes from the moment the carapace and the abdominal plates began to separate until the last leg was free. The time for molting agrees with observations by Mihara (1936) and Marukawa (1933) for immature king crabs. Takeuchi (1960) found that time for emergence of 13 immature crabs ranged from 8 to 40 minutes, and averaged 17 minutes. Personnel of the Fisheries Agency of Japan (1963 a) measured the time for molting at three to six minutes and observed no molting that took longer than 10 minutes. As Takeuchi (1960) pointed out, the differences in times recorded for molting may arise from the use of different reference points by various investigators for the start and end of molting.

Upon completion of molting, linear measurements were made at ½-hour intervals until maximum size had been attained. The increase, as a percentage of total growth attained for one molt, is shown in Figure 8. The king crabs attained an average of 53 percent

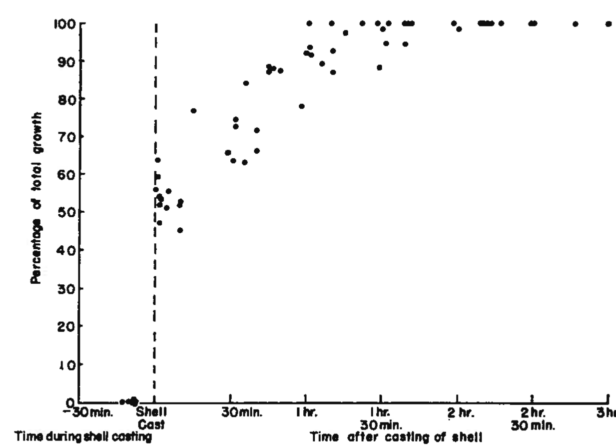

FIGURE 8. Percentage of total growth attained for one molt at varying time intervals after molting. Data from 12 crabs 29 mm to 39 mm in carapace length prior to molting.

of their growth by the time they had completely withdrawn from the old exoskeleton. This value agrees closely with observations on *Cancer magister* by Cleaver (1949) and Waldron (1958), who noted that 55.3 and 60 percent, respectively, of the linear growth was accomplished by completion of molting. By the time the exuvia is completely cast the previously distended abdomen has regained its flat intermolt form. Approximately 1½ hours elapse, however, before the carapace is completely expanded. The period of postmolt expansion apparently depends on the size of the individual; it is less for crabs smaller than those depicted in Figure 8 and greater for larger sizes. Sakuda (1958) reported that mature female crabs 115 mm to 141 mm in carapace length continue to expand for two days after molting.

Growth Increment

Growth increments for 317 molting king crabs are shown in Figure 9. Crabs 4 mm to 62 mm (carapace length) prior to molting show an average increase in

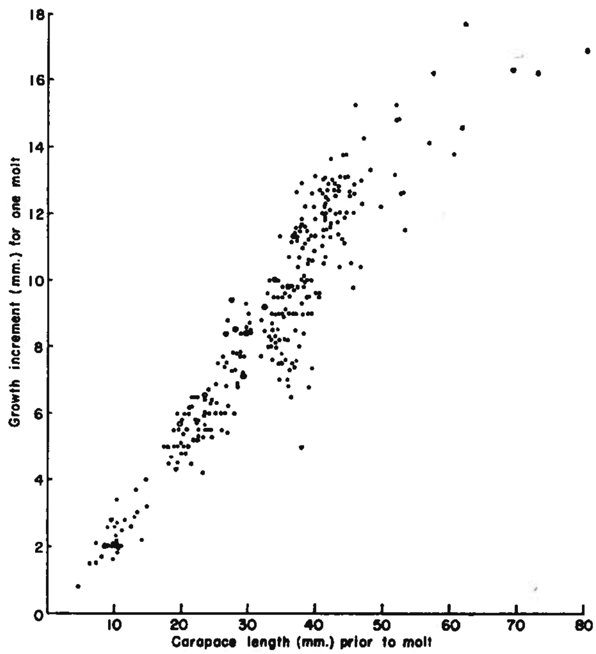

FIGURE 9. Growth increment per molt for 317 king crabs collected in the vicinity of Unalaska in 1958 and 1959. Open circles represent 12 crabs which molted prior to collection.

length ranging from 23 percent at 10 mm to 27 percent at 50 mm. The three observations beyond 62 mm, though few, do not agree with the growth per molt of smaller crabs and suggest a general decline in the percentage growth to about 20 percent at a carapace length of 80 mm. As is demonstrated later through an analysis of modes in size-frequency distributions, the growth per molt for immature king crabs over 60 mm long appears to remain at a nearly constant value of about 16 mm.

The literature contains a body of information on growth per molt of king crabs. The earliest observations on molting were published by Kajita and Nakagawa (1932), Mihara (1936), and Marukawa (1933), who retained immature crabs in holding cages and laboratory aquaria. Later, Sato (1958) and Bright *et al.* (1960) recorded growth per molt of immature crabs held in live boxes. Recently Takeuchi (1960) and Fisheries Agency of Japan personnel (1963 a) observed molting of immature crabs takenni Bristol Bay and held in rearing tanks aboard a factoryship.

Kurata (1961 b) reviewed the work of other investigators studying growth of immature king crabs in waters near Hokkaido and summarized their results. The combined results of the change in length at molting for Hokkaido crabs are expressed by the equation: $L_{n+1} = 0.353 + 1.086\,L_n$, where L_n is the premolt length at any given molt (n), and L_{n+1} the postmolt length. The slope (1.086) in the above equation is slightly less than that calculated from Tables 18 and 19 of Bright *et al.* (1960) for Cook Inlet crabs. The relationship at Cook Inlet, for 47 immature crabs 21 mm to 53 mm long, is expressed as: $L_{n+1}=1.162 +1.105\,L_n$. Recent studies of king crabs from the Bering Sea by Takeuchi (1960) and personnel of the Fisheries Agency of Japan (1963 a) indicate a greater growth per molt than did studies of either Kurata (1961 b) or Bright *et al.* (1960). Calculations from Table 1 of Takeuchi (1960) (observations on 31 crabs 8 mm to 17 mm long) result in the equation: $L_{n+1}= 0.012+1.183\,L_n$. Fisheries Agency of Japan (1963 a) presented results of increase per molt as: $L_{n+1}= -0.035+1.22\,L_n$, for 36 observations on crabs ranging from 8 mm to 26 mm long. None of these studies gave indication of differences between the growth per molt of male and female immature crabs, and all authors have combined the sexes in their reports.

Data from measurements of premolt and postmolt stage king crabs at Unalaska are shown in Table 6. Three observations on molting of crabs longer than

TABLE 6. Basic statistics for regression analysis of premolt (L_n) on postmolt (L_{n+1}) lengths for 314 immature king crabs 4 mm to 62 mm, premolt length.

Sex	N	Slope b	Intercept a	Standard error about regression (mm)
Male	148	1.278	−0.375	1.216
Female	139	1.289	−0.737	1.273
Unknown[1]	27	1.296	−0.807	0.542
All molts	314	1.284	−0.590	1.131

[1] The sex of these 27 crabs (4.3 to 34.0 mm premolt length) was not recorded.

62 mm are not included since the growth per molt in the larger animals did not appear to conform linearly to the growth per molt of the smaller ones. The small values of standard error around each regression line reflect the close relationship between the two variables, L_n and L_{n+1}.

Since the maximum difference at any one point between the regression lines for growth in length of male and female crabs does not exceed 1 mm, and values for the slopes and intercepts do not differ significantly from one another, the data were combined. The single line ($L_{n+1} = -0.590 + 1.284\,L_n$) shows an appreciably greater slope for the growth of Unalaska king crabs than those given by other investigators for crabs of other areas.

As was pointed out earlier, most of the investigators cited expressed some doubt as to the validity of observations on growth in confined animals as compared to growth under unconfined conditions. Takeuchi (1960) compared the percentage growth of crabs he held and those held by Marukawa (1933) for varying periods of time; he found no appreciable decrease in percentage growth with time in Marukawa's data, but he did state that his own observations indicated a generally decreasing trend. Takeuchi observed that the amount of growth per molt for crabs molting within one to five days after capture averaged 20 percent; for crabs held six days or longer before molting the average amount of growth attained at one molt was 16 percent—a difference of four percent.

Two assessments may be made of the effect of confinement on growth of immature king crabs collected at Unalaska. One is based on the comparison of growth at molting with duration of holding. The other compares the growth per molt of 12 immature king crabs which molted prior to collection with the growth per molt of crabs which molted in confinement.

Upon capture, crabs were placed indiscriminately into three holding cages and retained until completion of each sampling period. The longest period of holding was 46 days in the first sampling period. Maximum duration of holding for periods 2, 3, and 4 were 15, 14, and 10 days, respectively. Of the crabs which molted in confinement, more than 80 percent cast their shells within 15 days after collection. Knowing the date sampling commenced we can isolate some of the effect of confinement on growth by comparison of the growth of crabs which molted within five days after the first sample was taken with those which molted at a later date. The solid circles in Figure 10 represent 42 crabs which molted within one to five days after capture. The equation for these 42 observations is: $L_{n+1} = -0.124 + 1.273\,L_n$, which is very similar to the equation for all other crabs molting in confinement ($L_{n+1} = -0.764 + 1.288\,L_n$).

The other method of assessing the effect of confinement on the amount of growth per molt is based on comparison of the growth per molt of king crabs which were collected shortly after molting with the growth per molt of crabs which molted in confinement. As mentioned previously, 12 immature crabs and their cast shells were collected shortly after they had molted. Because the carapaces of these crabs did not increase

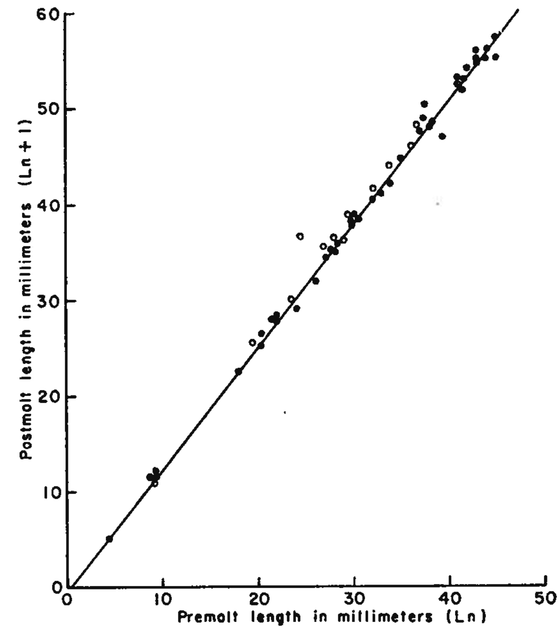

FIGURE 10. Premolt and postmolt lengths of immature king crabs collected at Unalaska. Open circles represent 12 crabs which molted before collection. Closed circles represent 42 crabs which molted one to five days after collection. The regression line ($L_{n+1} = -0.764 + 1.288\,L_n$) is for 260 crabs which molted six to 46 days after collection.

measurably after collection, molting must have occurred at least two hours prior to capture (see Figure 8). The unconfined crabs were caught near the locality where the holding cages were placed; thus environmental conditions were similar for both confined and unconfined groups. The premolt and postmolt measurements of these unconfined crabs are depicted by the open circles in Figure 10. The regression equation for these 12 individuals is: $L_{n+1} = 0.437 + 1.287\,L_n$. The 12 observations do show a consistently greater growth per molt than the confined crabs, but they are within the range of growth for confined individuals. The growth per molt of confined crabs is similar therefore to growth per molt under unconfined conditions.

Relationship Between Length and Width of Carapace

Changes in carapace form that accompany increase in size are not only evident at maturity but during the immature stage as well. From emergence of the first young adult form to a length of 20 mm, the carapace length in both sexes is greater than the width, but beyond 20 mm the width is greater than the length. Data on length and width of male and female immature crabs collected at Unalaska are given in Table 7.

TABLE 7. Basic statistics for analysis of length on width of immature male and female king crabs collected at Unalaska. Length range, 9-64 mm.

Sex	*N*	Slope *b*	Intercept *a*	Standard error about regression (mm)
Male	360	1.082	−1.439	1.302
Female	172	1.070	−1.216	0.629
Combined sexes	532	1.080	−1.449	1.132

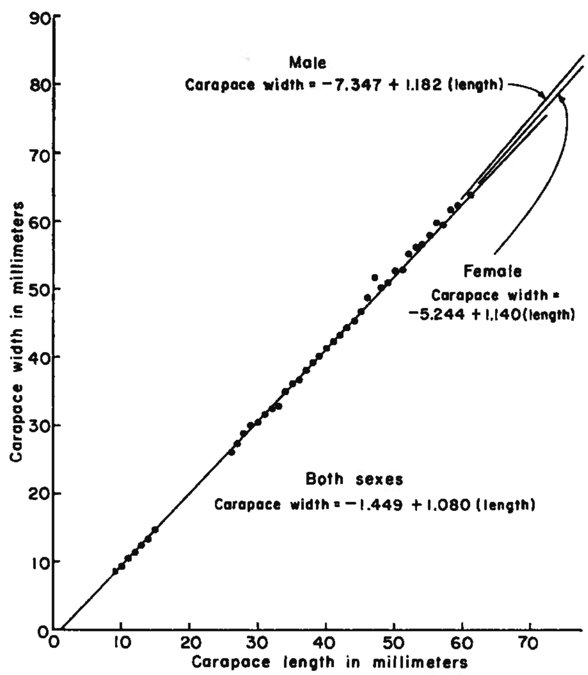

FIGURE 11. Length-width relationship of immature king crabs from Unalaska and the Bristol Bay region. Points represent average values, by 1 mm groups, of 532 Unalaska crabs. The regression line was fitted to the points by least squares. The two regression lines extending from 60 mm to 85 mm length represent length-width data from male and female crabs collected in Bristol Bay, and are identical to those presented in Figure 7.

The slope and intercept values for the sexes are not significantly different. Therefore, the length-width data for male and female king crabs were combined and may be expressed by the linear equation: carapace width $= -1.449 + 1.080$ (carapace length). The average carapace widths by 1-mm length intervals for king crabs 9 mm to 62 mm long are plotted in Figure 11, which is based on data presented in Table 8.

In earlier discussions of changes in the length-width relationship at maturity (see Figure 7), immature king crabs from the Bristol Bay region (55–85 mm long) showed different values in the regression equation than those above. The regression lines for male and female crabs from Bristol Bay are plotted in the upper portion of Figure 11. It is interesting to note that a slight flection occurs at a length of 55 mm to 60 mm. Because the length-width data for crabs from Bristol Bay and Unalaska barely overlap, the presence of a flection point as indicated by these data alone is not conclusive. Data from other sources suggest, however, that the flection is real.

TABLE 8. Length-width relationship for 532 immature king crabs collected at Unalaska in 1958–59.

Carapace length (mm)	Average carapace width (mm)	*N*
9	8.7	5
10	9.5	15
11	10.7	20
12	11.5	26
13	12.7	28
14	13.6	14
15	14.9	7
26	26.3	3
27	27.5	6
28	28.8	5
29	30.3	9
30	30.7	17
31	31.9	12
32	32.8	10
33	33.3	16
34	35.4	10
35	36.6	19
36	37.1	17
37	38.4	24
38	39.6	17
39	40.5	22
40	41.6	16
41	42.4	14
42	43.5	14
43	44.6	17
44	45.5	11
45	47.1	7
46	49.0	6
47	50.0	4
48	50.6	5
49	51.2	5
50	53.0	11
51	53.2	5
52	55.4	8
53	56.4	9
54	56.8	32
55	58.2	16
56	59.8	12
57	59.7	19
58	61.8	8
59	62.4	5
60	—	—
61	64.3	6

Figure 2 in Marukawa (1933) shows a change in the ratio of width to length at a width of approximately 60 mm (62 mm length), and the same is noticeable in his Figure 3, a comparison of carapace width to rostrum length. Figure 12 of the present study is based on data from Takeuchi (1960, Table 1), Bright

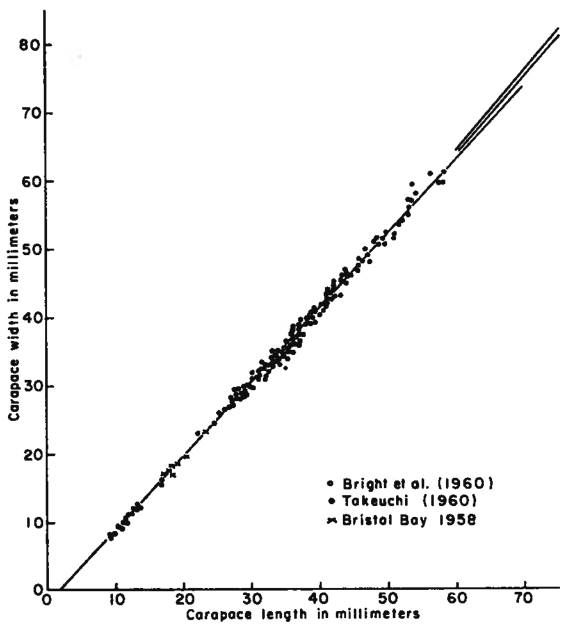

FIGURE 12. Length-width relationship of immature king crabs from the southeastern Bering Sea and the Gulf of Alaska. Data from Bright *et al.* (1960, Tables 25 and 27) for Cook Inlet crabs. Data for the Bristol Bay region from Takeuchi (1960, Table 1), and collections by the U.S. Fish and Wildlife Service in 1958. Regression lines are the same as those of Figure 11.

et al. (1960, Tables 25 and 27), and observations in Bristol Bay by the U.S. Fish and Wildlife Serice in 1958. The regression lines are those depicted in Figure 11. The length-width ratio of immature king crabs from Unalaska is clearly similar to that of crabs of Cook Inlet and the Bristol Bay fishing region. Thus, the presence of a flection at a length of 55 mm to 60 mm does not appear to be attributable to a difference between crabs in Bristol Bay and Unalaska, but is most likely a change taking place in the length-width relationship.

A change in allometric growth within the immature phase has been noticed in other decapod Crustacea. Teissier (1960) presents data on the brachyuran crab, *Maja squinado*, which indicates a prematurity change in the relative growth of the claw in relation to carapace length. This change in relative growth indicates the attainment of the prepubertal stage, at which time sexual differences begin to appear. In a discussion of various Crustacea, Teissier (1960) mentioned that morphological changes in the male are more pronounced than in the female during the prepubertal stage—female features generally remaining in accordance with previous dimensions. These remarks agree with observations on immature king crabs. Thus, the immature stage in king crabs may be divided into two length phases; the first extends from 2 mm to 60 mm, and the second (prepubertal) from 60 mm to maturity.

Changes in Weight at Molting

Rigidity of the exoskeleton prevents a change in linear dimensions except at molting, but the same is not true of body weight even though volume remains constant between molts. At time of molting, weight increases rapidly through absorption of water. The water is then replaced by soft tissue before the next molt. Since body tissue is heavier than the water absorbed, the increase in weight for any one molt lags behind the linear increase. Figure 13 shows weight in grams, by length, of 72 premolt king crabs prior to absorption of water, and 36 postmolt crabs two days after molting. The postmolt crabs consistently weigh less than premolt individuals of comparable length. Thus, calculation of the actual gain in weight per molt depends in part upon the point in the molting cycle when weight measurements are taken.

The average length-weight relationship for immature king crabs at Unalaska in the latter part of the intermolt stage is shown in Figure 14. A curve fitted

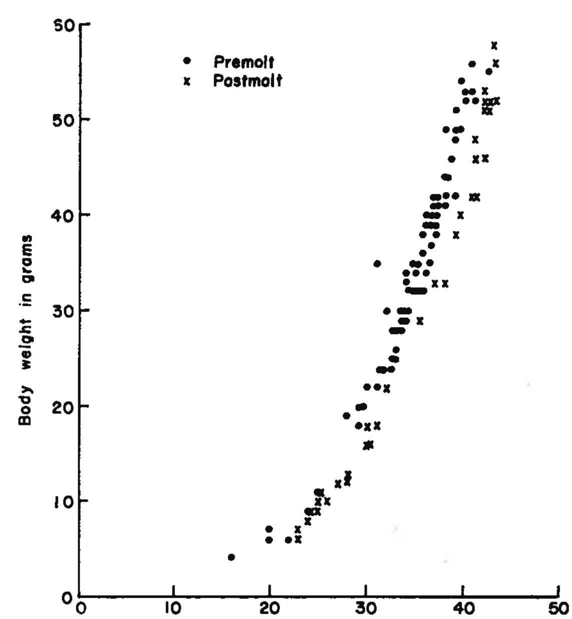

FIGURE 13. Length and weight of 72 king crabs in the premolt stage, and 36 crabs in the postmolt stage. Collections at Unalaska.

TABLE 9. Length-weight relationship for 850 immature king crabs collected at Unalaska in 1958–59.

Carapace length (mm)	Average body weight (g)	N
9	0.5	5
10	1.0	9
11	1.1	29
12	1.3	64
13	1.7	62
14	2.1	35
15	2.3	11
16	2.7	4
17	3.0	3
18	4.2	10
19	5.0	7
20	5.5	22
21	6.2	14
22	6.8	26
23	7.3	17
24	8.7	18
25	10.1	20
26	11.1	16
27	12.9	31
28	13.7	24
29	15.5	15
30	17.2	31
31	19.3	13
32	21.6	16
33	24.6	11
34	27.1	7
35	31.1	20
36	33.8	23
37	36.0	33
38	39.6	37
39	43.6	41
40	47.2	35
41	49.0	25
42	51.7	23
43	54.2	22
44	59.1	16
45	61.6	20
46	67.2	13
47	71.8	6
48	75.6	9
49	83.5	4
50	90.0	2

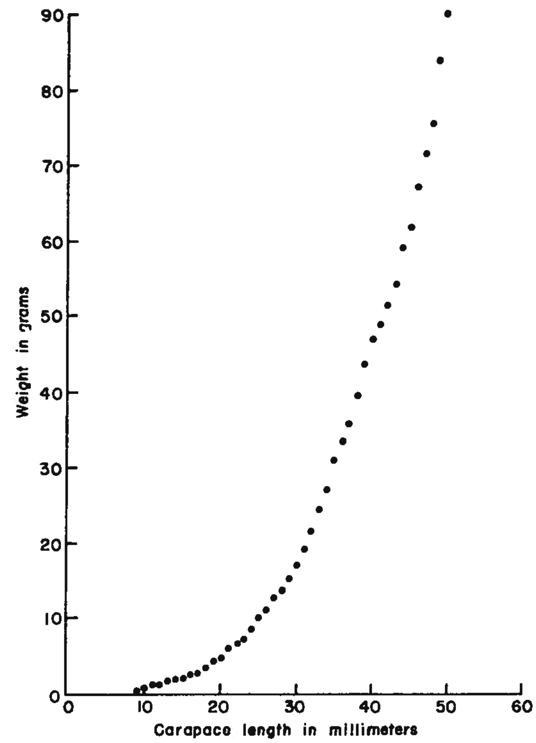

FIGURE 14. Length-weight relationship of 850 immature king crabs from 9 mm to 50 mm, carapace length. Points are average weights by 1 mm length intervals.

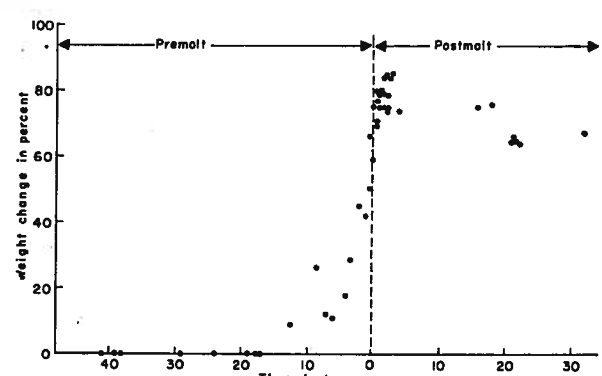

FIGURE 15. Percentage change in weight at molting of five immature king crabs 30 mm to 38 mm, premolt length. Points indicate the percentage change in weight as calculated from the premolt weight 20 or more hours prior to molting.

to the data represented by these points is expressed by the equation: $W=0.0012\ L^{2.937}$; where W is body weight in grams and L is carapace length in millimeters. The data from which Figure 14 was constructed are presented in Table 9.

Travis (1954) showed that body weight of the spiny lobster, *Panulirus argus*, increased an average of 10 percent just prior to molting. At molting there was a loss in body weight. This was attributed by Travis to the loss of the cast shell. The weight of *P. argus* begins to increase several hours after molting, but remains less than the premolt weight for two to four days following the molt. Such extreme fluctuations in body weight at molting were not noticed in immature king crabs. Figure 15 gives the weight change at molting of five immature crabs collected at Unalaska. The crabs were weighed at arbitrary intervals after being allowed to drain for two minutes. Weight con-

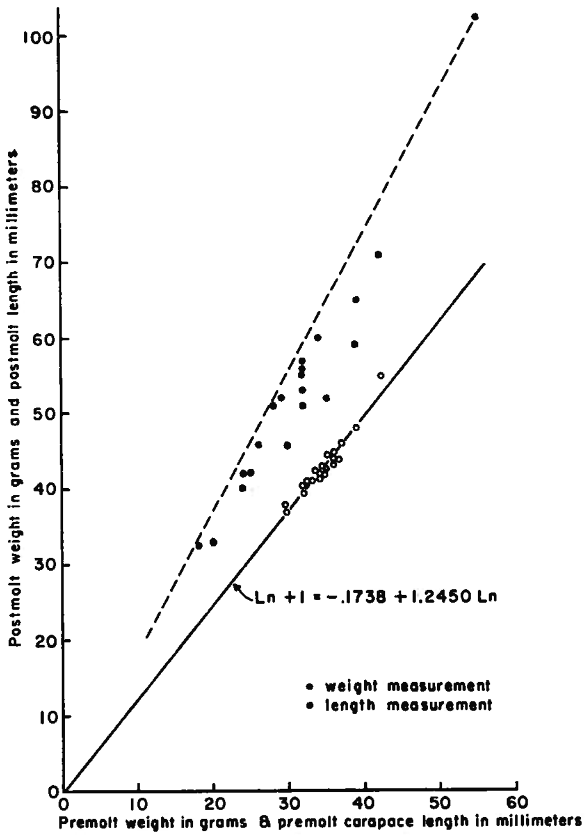

FIGURE 16. Premolt and postmolt weights and carapace lengths of 20 immature king crabs collected at Unalaska in the first sampling period. The regression (unbroken) line is based on 86 molting observations taken concurrently in the first sampling period. The broken line is the expected weight gain from intermolt stage to intermolt stage as derived from Figure 14.

tinues to increase for three to four hours after molting, and then decreases slightly during the next day. There is no evidence of loss in weight through casting of the old shell.

Figure 16 shows premolt and postmolt measurements of length and weight of 20 immature king crabs collected in the first sampling period (data are in Table 10). The average increases in length and weight for these individuals are 24.3 and 69.7 percent, respectively. The regression (unbroken) line, which represents observations of 86 molting crabs measured during the first sampling period, indicates that these 20 molting observations are representative of the average growth at this time. Weight measurements were taken prior to premolt swelling and from two to five days after molting. Because of the replacement of water by soft tissue before the next molt, the total weight gain for any one molt is slightly greater than that shown by the closed circles in Figure 16.

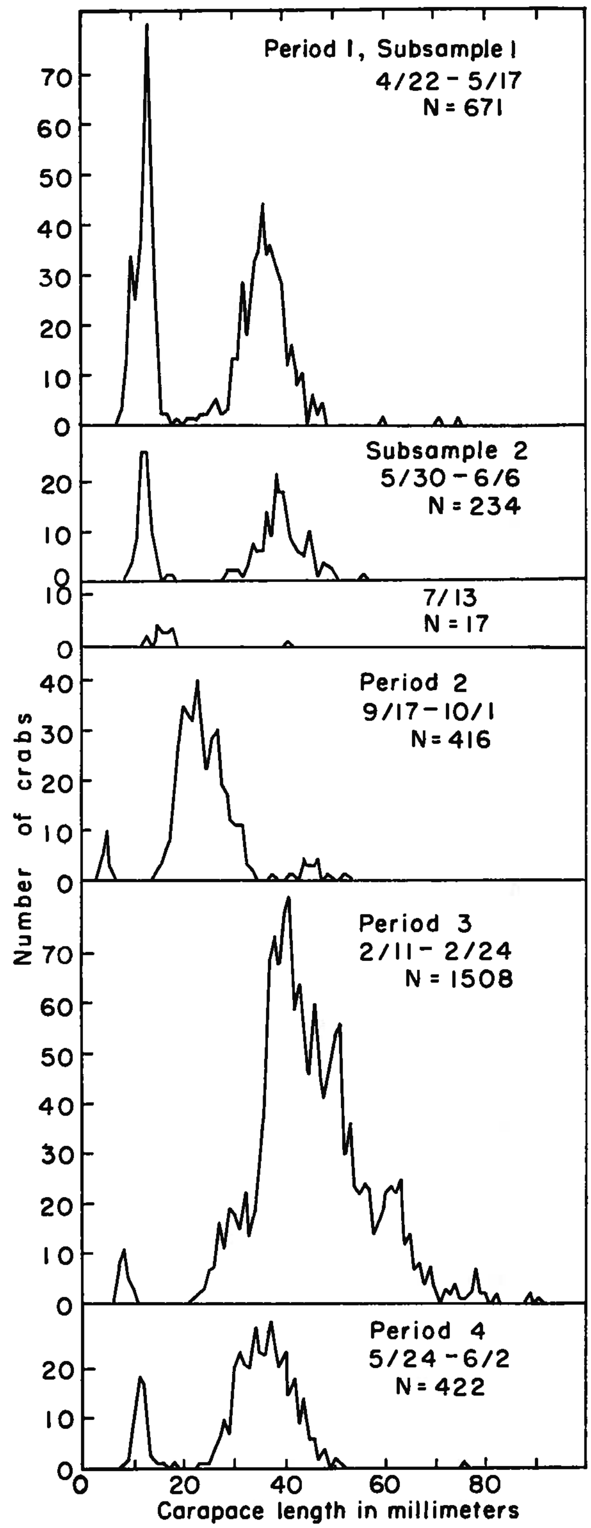

FIGURE 17. Length-frequency distribution, by sampling period, of immature king crabs collected in the vicinity of Unalaska in 1958 and 1959.

TABLE 10. Premolt and postmolt weights and carapace lengths for 20 immature king crabs collected at Unalaska in May and June of 1958.

Sex	Premolt Length (mm)	Premolt Weight (g)	Postmolt Length (mm)	Postmolt Weight (g)	Length increase (mm)	Length increase (%)	Weight increase (g)	Weight increase (%)
F	33.0	26	41.0	46	8.0	24.2	20	76.9
M	31.8	24	40.5	42	8.7	27.4	18	75.0
F	35.8	32	44.0	55	8.2	23.0	23	71.9
M	33.5	29	42.5	52	9.0	26.9	23	79.3
F	35.0	32	44.5	57	9.5	27.1	25	78.1
M	33.5	28	42.0	51	9.5	28.4	23	82.1
F	34.5	32	42.0	53	7.5	21.7	21	65.6
F	42.3	55	54.0	102	11.7	27.7	47	85.5
F	29.3	18	37.0	33	7.7	26.3	15	83.3
F	34.5	32	43.0	56	8.5	24.6	22	68.8
F	31.8	24	39.5	40	7.7	24.2	16	66.7
F	36.5	39	44.0	59	7.5	20.6	20	51.3
M	32.5	25	41.0	42	8.5	26.2	17	68.0
M	29.6	20	38.0	33	8.4	28.4	13	65.0
F	34.0	30	42.0	46	8.0	23.5	16	53.3
F	39.0	42	48.0	71	9.0	23.1	29	69.1
F	37.0	39	46.0	65	9.0	24.3	26	66.7
M	35.0	32	42.5	51	7.5	21.4	19	59.4
F	36.1	35	43.3	52	7.2	19.9	17	48.6
M	36.0	34	44.8	60	8.8	24.5	26	76.5
Average	34.5	31.4	43.0	53.3	8.5	24.3	21.9	69.7

The average expected weight gain from intermolt stage to intermolt stage is represented by the broken line. This line was calculated by determining the premolt and postmolt lengths, as based on the regression line, and the respective weights at these lengths as derived from Figure 14. The difference between the expected weight gain (broken line) and the observed weight gain (closed circles) is the amount of increase in body weight which is to be accrued before the crabs attain the next premolt stage. The difference amounts to an average of 10 percent.

Growth of Immature King Crabs at Unalaska

Length-Frequency Distribution in all Areas Sampled

King crab zoeae hatch in the early spring. Thus, the young of one year have ordinarily grown sufficiently by the next spawning season to be easily distinguished from the succeeding brood. Overlapping of year classes apparently does not occur during the immature phase; growth may be estimated therefore from changes in the position of modes in length-frequency distributions of repeated samples from the same population.

Figure 17 shows the length-frequency distributions by sampling period for all king crabs collected during the year of study at Unalaska. The basic data from which Figure 17 and the following four figures (18–21) are derived are presented in Appendix Table II. The first period of sampling, from April to June 1958, has been divided into two sub-sampling periods, one from April 22 through May 17, and the other from May 30 through June 5. A sample of 17 individuals was taken on July 13, 1958, but this is not considered a sampling period.

More than 95 percent of the king crabs collected during the year were captured in areas 1 through 4 (Figure 3). Of the individuals taken during periods 1 and 2, 93 percent were from area 2. The two modal groups first observed in April and May shifted progressively to the right during the summer, and a new modal group appeared at about 5 mm in September.

In the third period (February 11–24, 1959) the majority of crabs were taken from pods in areas 1 and 3. These pods were composed predominantly of premolt stage individuals. Division of the length-frequency distribution of period 3, by area and molting stage, is shown in Figure 18. Position of the premolt and postmolt modes for each group are also indicated in Figure 18. In group C the small number of crabs in the postmolt stage allows some doubt as to the actual existence of modes. Their presence is partly demonstrated by the fact that the differences in length between the premolt modes at 50 mm and 61 mm and the postmolt modes at 63 mm and 78 mm are consistent with the growth per molt noted in observations on molting. Individuals of the 47 mm and 60 mm modes of group D were classified as being in the premolt stage, but those making up the 29 mm length mode were predominantly in the postmolt stage. There does not appear to be a relationship between the premolt and postmolt modes of group D.

It should be pointed out that the term postmolt as used in this section includes not only those crabs which obviously molted recently but also includes crabs in the intermolt stage. Because the difference between early and late intermolt is often difficult to detect, it was decided to limit the premolt group to those crabs which were obviously in the premolt stage. Thus, the left-hand side of the postmolt length distributions may be composed to some extent of late intermolt stage individuals prior to entering the premolt stage. These individuals should be included within the premolt group. It is realized that this method of grouping may tend to shift the postmolt modal position to the left when late intermolt individuals are numerous. For the most part, however, the postmolt modes are discrete and any distortion is of a minor nature.

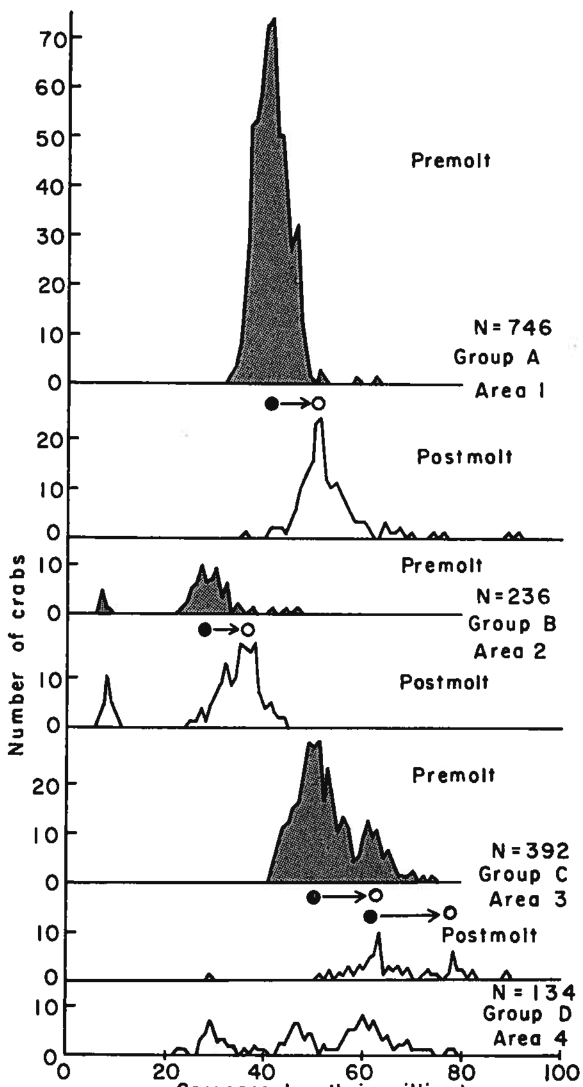

FIGURE 18. Length-frequency distribution, by sampling area (see Fig. 3) and molting stage, of immature king crabs collected in February 1959 (sampling period 3, Fig. 17); closed and open circles represent positions of premolt and postmolt modes and their advancement.

Of 422 king crabs collected during period 4 (May–June 1959) all but 12 were from areas 2 and 4. Figure 19 gives the length distribution of premolt and postmolt crabs for these two areas; the distance between modes is 2–3 mm less than the average growth observed at molting.

Some modes, especially those representative of pods in period 3, appear to be groups which were not sampled continuously. It is difficult to estimate the proper placement of a mode in relation to time when it has not been observed to progress in a size-time se-

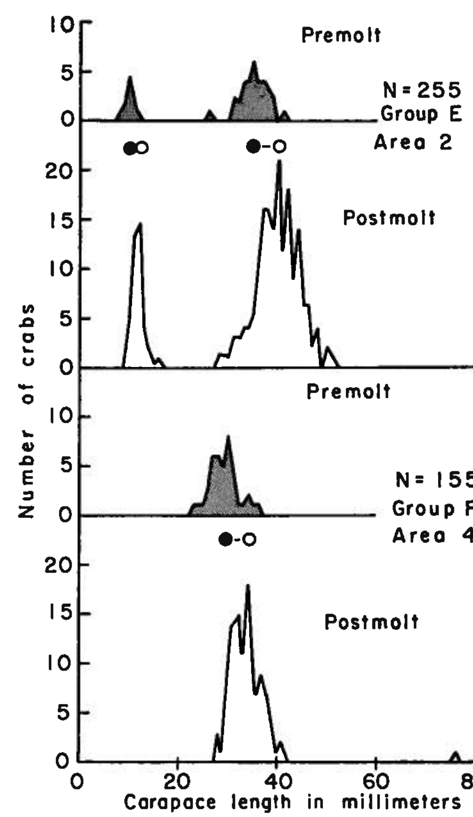

FIGURE 19. Length-frequency distribution, by molting stage, of immature king crabs collected in sampling areas 2 and 4 (see Fig. 3) during May-June 1959 (sampling period 4, Fig. 17); closed and open circles represent positions of premolt and postmolt modes and their advancement.

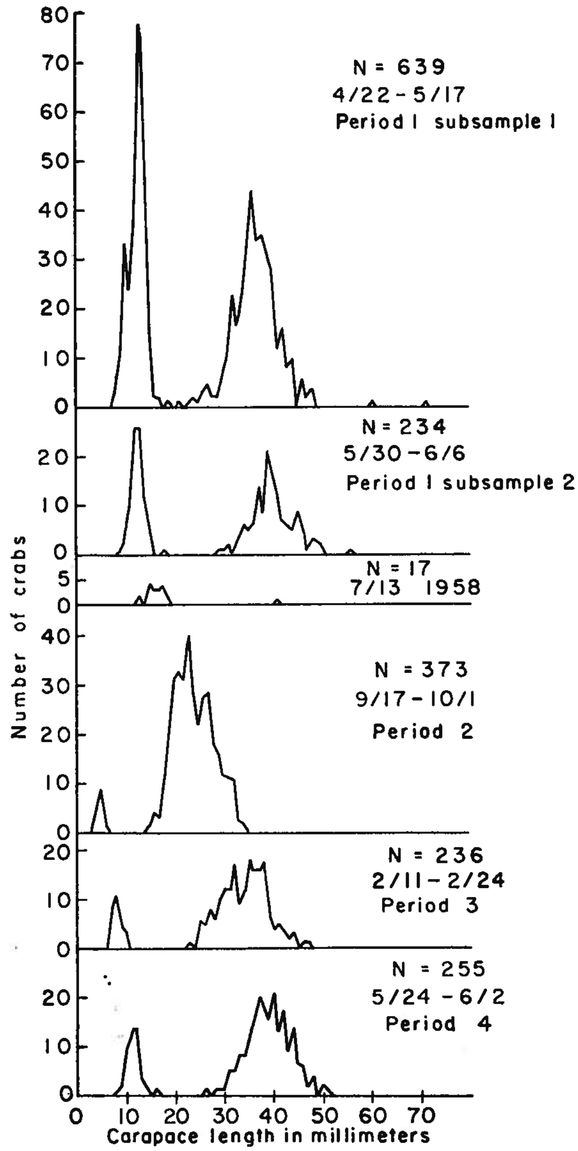

FIGURE 20. Length-frequency distribution, by sampling period, of immature king crabs collected in sampling area 2 (see Fig. 3).

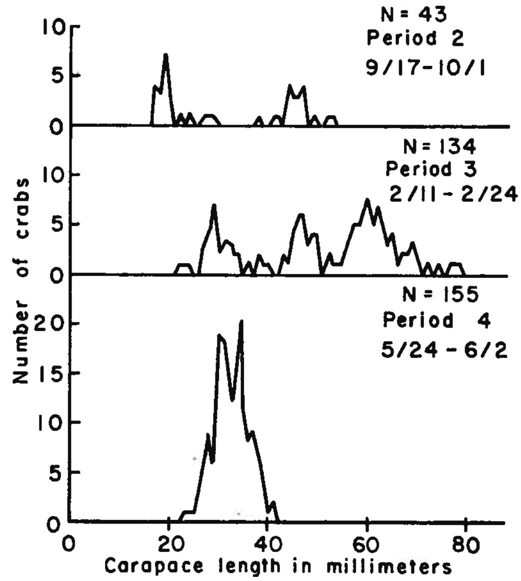

FIGURE 21. Length-frequency distribution, by sampling period, of immature king crabs collected in sampling area 4 (see Fig. 3).

quence. Since the only reliable means of determining what the modes in a sample represent is by following their progression, it is appropriate to consider first an area which was consistently sampled through the year and then to interpret data for the other groups in accordance with these results. Samples were collected in area 2 during each sampling period and in area 4 during the last three periods. Data from these samples will be used to demonstrate modal progression.

Length-Frequency in a Single Area

Figure 20 shows the length-frequency distribution of king crabs collected in area 2. Two modes are evident in the first subsample of period 1, one at 13 mm and the other at 36 mm. The smaller mode, at 13 mm, progressively shifts to the right with each successive sampling period. The mode at 5 mm that appeared in period 2 is evident at increased sizes in the following two sampling periods. In the fourth period two modes are again present in relatively the same positions as those in period 1.

Immature king crabs collected in area 4 during sampling periods 2, 3, and 4 and their size-frequency distributions are shown in Figure 21. Crabs of the 60 mm length mode of period 3 were taken only once and appear to be members of a pod moving through the area. In a survey of this area two days later, only cast shells 53 mm to 69 mm long were seen.

To establish the relation of the modes shown in Figures 20 and 21 to age it is necessary to determine a base point. As mentioned earlier, hatching of king crab zoeae in the vicinity of Unalaska occurs about mid-April, and the first young adult form is probably present by early July. As is shown in Figure 2, there is general agreement in published reports that immature crabs at the age of one year are approximately 10 mm long. Nakazawa (1912) found numerous immature crabs that averaged 10 mm long in Nemuro waters during the later part of May. From observations of the presence of king crab zoeae during May and June, Nakazawa inferred that the 10 mm individuals must have hatched one year previously. These findings agree with those of Marukawa (1933) who, through rearing experiments and collection of immature crabs in nature, concluded that 1-year-old crabs were 7 mm wide (8 mm long). On the basis of these estimates it seems reasonable to expect that a crab hatched at Unalaska in mid-April would be 2 mm long in early July and near 10 mm long one year after hatching.

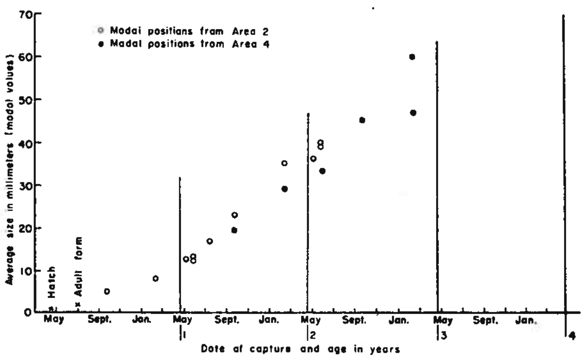

FIGURE 22. Modal values, by date of capture, of immature king crabs collected in sampling areas 2 and 4 (see Fig. 3) in 1958 and 1959.

Progression of Modes and Growth

Progression of modes is demonstrated in Figure 22, which is a plot, by date of capture, of the modal values of the one continuously present year class shown in Figure 20. This year class was first observed in early May 1958 when the modal length was 13 mm. Since king crabs near 10 mm long are probably one year old, the 13 mm crabs at Unalaska are considered to be slightly older than one year. The modal values for the year class, by date of sampling throughout the year, are shown by the open circles in Figure 22. The points extend from May at age 1 to June at age 2. In September 1958 (period 2) another distinct group of crabs 4–6 mm long was collected. This group is considered to be a younger year class whose modal values are also shown as open circles in Figure 22. These points are plotted from September of the year of hatching through June at age 1. Open circles plotted in May and June at age 2 represent the modes of larger crabs taken during the first sampling period. These modes, as plotted, complete a growth record of more than two years in duration.

With this basic relationship between size and age established, the modes representative of area 4 (Figure 21) were plotted in Figure 22 as closed circles. King crabs constituting the 60 mm mode of period 3 were regarded as less than three years old. The argument for considering these 60 mm crabs as 2-year-olds nearing three years rather than 3-year-olds is twofold: the general growth trend as depicted by modal values of smaller crabs indicates an expected size of 60 mm at age 3; a size of 60 mm at nearly age 4 would require a flection at approximately 40 mm. On the basis of data presented on allometric growth, and on the amount of growth per molt, a flection occurs at 60 mm rather than at 40 mm. Also, almost all the individuals comprising the 60 mm mode were in a premolt condition and actively molting, as is evidenced by the number of cast shells found in subsequent sampling. Results of our observations on molting show that a 60 mm crab would be about 76 mm long after molting. If this group of crabs had been available for sampling several days later, we would expect to find a modal value at 76 mm, a size more in accordance with the growth trend for crabs almost four years old.

Throughout the year of sampling, consistently large numbers of king crabs were found to be in either the premolt or postmolt stage. Therefore, if the samples had been taken two weeks earlier or later the modes observed would have been in different positions. The amount of variability expected in determining growth

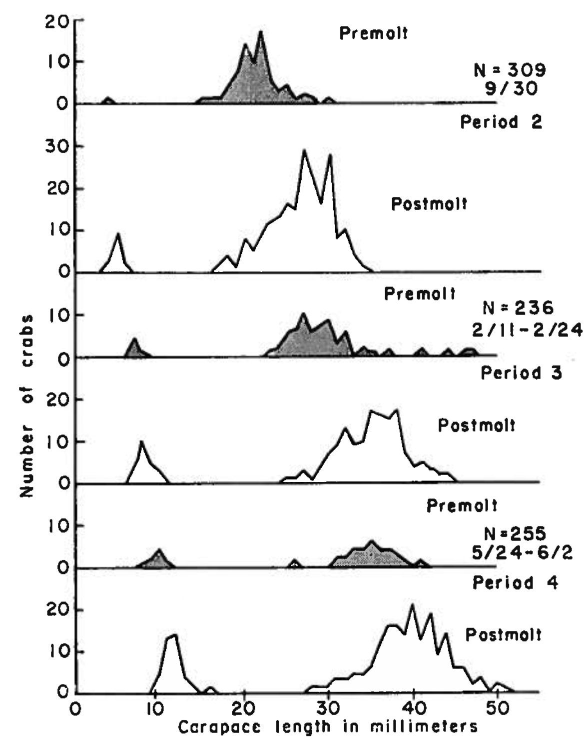

FIGURE 23. Premolt and postmolt modes, by sampling period, of immature king crabs collected in sampling area 2 (see Fig. 3).

by modal values may be assessed by analysis of premolt and postmolt modes. Figure 23 presents the length-frequency distributions of Figure 20 divided into premolt and postmolt groups. Shell condition was not recorded in the first sampling period. Shell condition was recorded at the end of sampling period 2 on September 30, 1958, not at the time of collection.

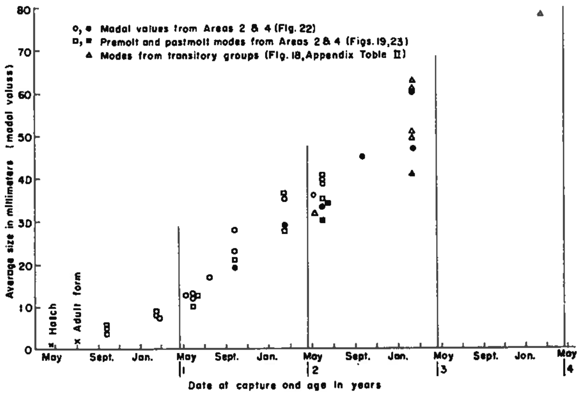

FIGURE 24. Modal values, by date of capture, of immature king crabs collected in all areas at Unalaska in 1958 and 1959.

On September 30, those crabs which had not molted while in confinement were measured, and shell condition was recorded. Data for periods 3 and 4 are taken from groups B and E of Figures 18 and 19, respectively. The premolt and postmolt modes from area 2 (Figure 23) are shown as open squares in Figure 24. The two solid squares at lengths of 30 mm and 34 mm in June at age 2 represent the premolt and postmolt values of group F (area 4) in Figure 19.

After separation of each length mode into premolt and postmolt groups, and plotting the modes of these groups on their respective sides of the unseparated length modes (as shown in Figure 24), it was possible to estimate the amount of variation in length expected in analysis of progression of modes. This variation is calculated to be approximately plus or minus 15 percent of the values of the unseparated length modes. The expected variation of 15 percent is actually less than is indicated in Figure 24, for the postmolt modes would be shifted to the right and the premolt modes to the left. This shifting would compensate for the time at which the majority of crabs would have been, or were, at a different size. The amount of shift is dependent upon molting frequency.

During the year of sampling, several groups of king crabs 30 mm to 80 mm long were not sampled continuously and are interpreted as being transient. The positioning of modes of these transient groups can only be approximated by using the previous results as a base point. In May of the first sampling period, 20 individuals were captured in one lift of a 2-inch mesh tangle net. The carapace lengths (Appendix Table II) of this group ranged from 29 mm to 35 mm, and had a mode at 32 mm. This mode is shown in Figure 24 as a triangle in May at age 2. In period 3 (February 1959) immature crabs were collected from two pods. The premolt and postmolt modes for these pods were at lengths from 41 mm to 78 mm, and are shown as groups A and C in Figure 18. For group A the premolt mode was at 41 mm and the postmolt mode at 51 mm. The combined size-frequency distribution for this group was bimodal; lengths ranged from 35 mm to 60 mm, and averaged 46 mm. In view of the size range and average length of 46 mm, the crabs represented by these premolt and postmolt modes are most reasonably classed as between age 2 and age 3; they have been plotted as triangles in Figure 24. The 50 mm premolt length mode and the 63 mm postmolt length mode of group C are also considered as being composed of crabs almost age 3. Crabs represented by the premolt mode at 61 mm (group C) have been designated as 3-year-olds, and the postmolt mode crabs as 4-year-olds. As is demonstrated later from length distributions of immature crabs collected in sampling surveys in Bristol Bay, crabs longer than 60 mm apparently molt annually. Values of the modes of the transitory groups, if plotted correctly in relation to time, extend the growth record to include the first four years of life.

A resume of results on growth of immature king crabs as determined by the Unalaska study is given in Table 11. The average lengths at the end of the first and second years of life are well defined, but the lengths at the end of the third and fourth years are not as distinct; they have been estimated in part by extrapolation of the growth trend observed for the smaller and younger crabs.

TABLE 11. Average length by age of immature king crabs in the vicinity of Unalaska, Alaska.

Age (years)	Aver. length (mm)	Range (mm)
1	11	9–14
2	35	29–41
3	60	50–67
4	80	—

GROWTH OF IMMATURE KING CRABS IN BRISTOL BAY

Length-Frequency Distribution

From 1955 through 1961 the U.S. Fish and Wildlife Service conducted an offshore survey of king crabs of the Bristol Bay fishing region. In each year except 1955 and 1956, quantities of immature crabs were collected. The length distributions of male crabs less than 120 mm long, and female crabs less than 110 mm long, are shown in Figure 25. Growth of male crabs longer than 120 mm has been reported by Weber and Miyahara (1962). Length distributions for female crabs longer than 110 mm are not given since at larger

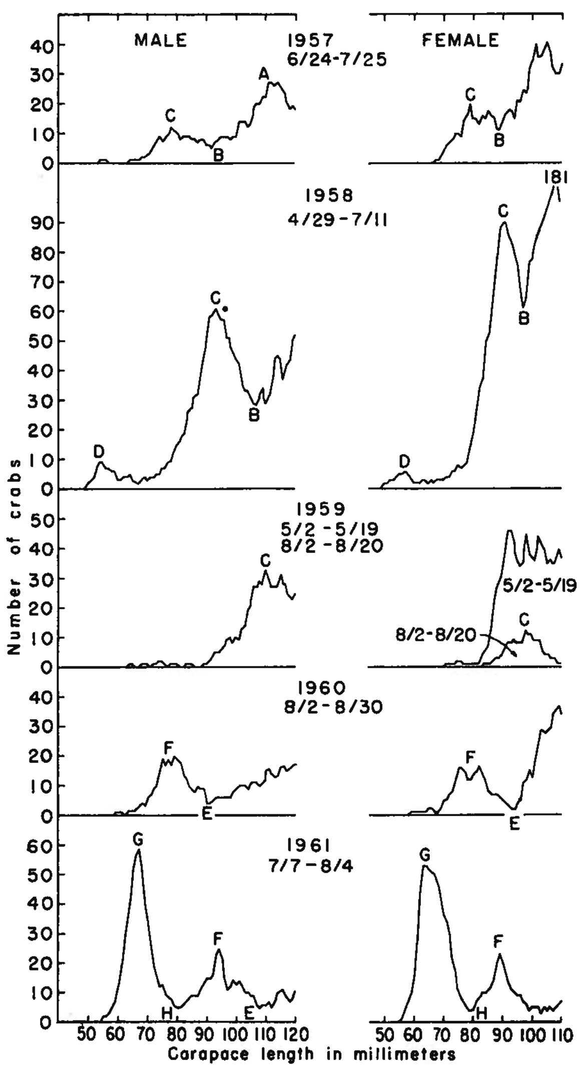

FIGURE 25. Length-frequency distributions of Bristol Bay male and female king crabs by sampling year.

sizes the reduced amount of growth per molt in females produces such overlapping of distributions of age groups that modes of individual groups become unidentifiable.

The length-frequency distributions show the presence and progression of both dominant and poorly represented groups. For convenience of discussion these groups are listed alphabetically by year of entry in the samples; the same letter identifies corresponding groups of each sex. Before the progression of these groups is considered, several points should be clarified. The king crab survey of 1959 took place in early spring and sampling of females was conducted before the majority had completed molting. Early sampling caused the length distribution of females in 1959 to be similar to the distribution of females in 1958. In August 1959 additional females were collected during a tagging program. The length-frequency distribution of females taken after molting was completed showed a mode at 98 mm. In 1958 immature crabs less than 60 mm long were numerous in the sample. In general, immature crabs do not appear on the fishing grounds until they attain 70 mm length and then are noticeable only if they constitute a particularly strong year class. Also, because of the gregarious behavior of immature crabs, a mode may represent a single trawl catch. For example, the individuals that made up mode D were collected in a single trawl haul near Port Moller. Since crabs less than 60 mm long were not collected at other locations in the 1958 survey, and mode D is not represented at an increased length in 1959, it is questionable whether the mode represented a distinct year class. The same situation applies to individuals comprising mode G in the 1961 sample. The majority of these immature crabs were taken in one haul near Port Moller. Immature crabs 60–70 mm long were encountered, however, in other trawl hauls in 1961, indicating that this mode is more likely to be representative of the average size of a dominant year class.

Progression of Modes

Figure 26 shows the positions of the dominant and poorly represented size groups of Figure 25 by their

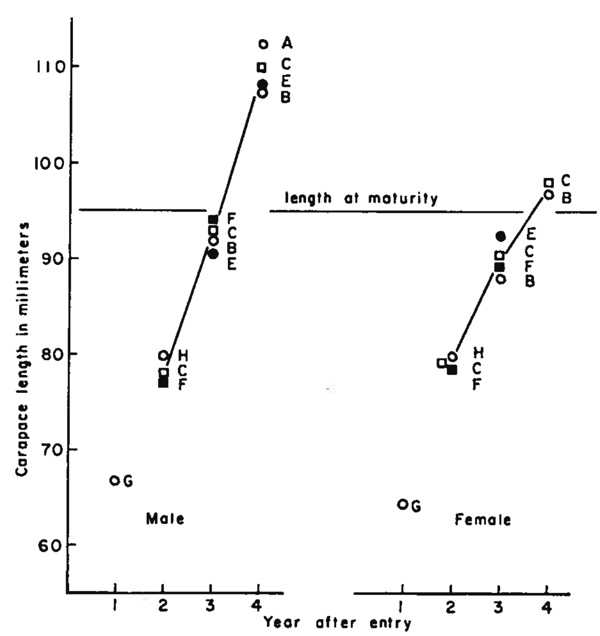

FIGURE 26. Progression of dominant and poorly represented size groups in Bristol Bay king crabs by their year of entry in the length-frequency distributions. The letters designate the groups shown in Figure 25, and the solid line shows the average progression of these groups.

year of first entry in the samples. The distance between these groups from one year to the next agrees with observations on molting at Unalaska, and results of tag returns for immature king crabs in the Gulf of Alaska. Powell (1960 a) found that tagged immature king crabs (74–91 mm long at release) in the Gulf of Alaska averaged 16 mm per molt; the same growth per molt as noted in the Unalaska studies. Advancement of modes in Bristol Bay approximates this figure; thus immature king crabs must molt only once a year after attaining a carapace length of 60 mm to 70 mm.

The position of modes in Figure 26 is not plotted by date of sampling within the season for the following reasons: Mature female king crabs molt in April and May in the Bristol Bay region; the season at which mature male crabs molt is uncertain, but it is believed to be late winter or early spring (Weber and Miyahara, 1962). Newly molted immature crabs were found infrequently, and only in early spring, in Bristol Bay. From analysis of tag returns in the Gulf of Alaska, Powell (1960 a) believes that molting of immature king crabs longer than 70 mm occurs primarily during February and March. Since immature crabs, after attaining a length of 60–70 mm, molt annually, their size remains constant from the time of molting in the early spring throughout the period of sampling. Thus, the length-frequency distributions of Bristol Bay crabs collected throughout the summer are indicative of the size taken at any time after molting is completed.

If each mode is held to represent an age group, the average annual increase in length is almost constant for male crabs in Bristol Bay. For female king crabs of Bristol Bay, a lesser rate of annual increase is evident, especially after maturity.

Growth of Immature King Crabs of the Southeastern Bering Sea

The 1958–59 study at Unalaska covered the growth of king crabs from time of hatching to a carapace length of 80 mm. The Bristol Bay region data included crabs of 65 mm through maturity at 95 mm. Combination of these two sets of data should give a comprehensive growth curve for immature king crabs.

Time of hatching and rate of larval development in the Bristol Bay region cause a delay of about six weeks in the time of appearance of the first adult form as compared with Unalaska. If the growth pattern of immature king crabs at Unalaska is retarded six weeks to compensate for the later development of Bristol Bay larvae, the difference at any one point in the estimated average length does not change by more than 2 or 3 mm. This difference is less than the range of variability shown by these data with the method of analysis employed.

Figure 27 shows the combined data of the Unalaska studies (Figure 24) and the modal values in Bristol Bay (Figure 26). The base point for determination of age is derived from the time of hatching as judged from the Unalaska data. Individuals comprising the Bristol Bay group at a length of 65 mm have been designated as 3-year-olds. Age-length relationships compiled from averages of the combined data are given in Table 12 and are presented graphically in Figure 28.

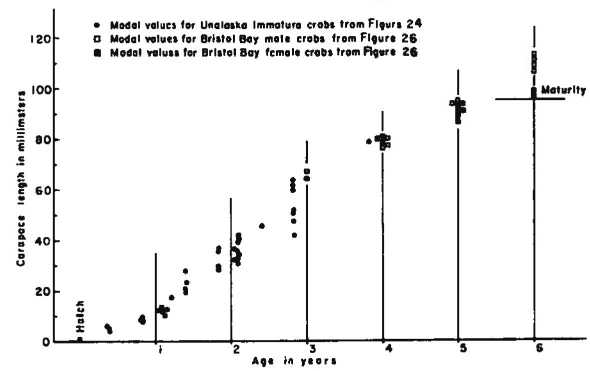

FIGURE 27. Modal values of immature king crabs in relation to age as estimated from length distributions at Unalaska and in Bristol Bay. Time of hatching is based on Unalaska data.

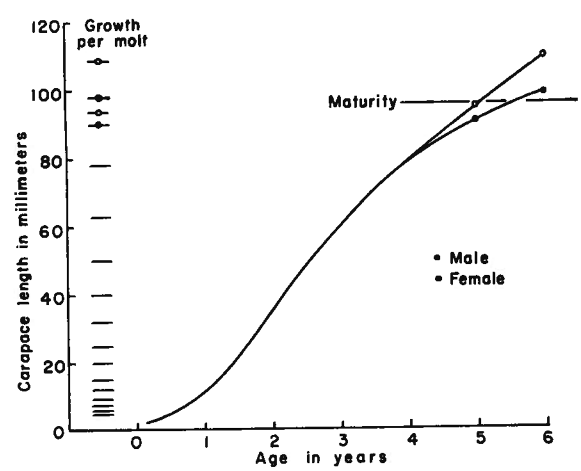

FIGURE 28. Growth curve for immature king crabs of the southeastern Bering Sea. Carapace lengths and corresponding ages are based on modal values shown in Figure 27. Cumulative growth per molt for immature crabs 5 mm and longer is shown to the left.

After an age-size relationship is determined for immature king crabs, the number of molts required to attain a given age may be calculated. Cumulative growth per molt, as determined from molting observations at Unalaska and length distributions in Bristol

TABLE 12. Average length by age of immature king crabs of southeastern Bering Sea.

Age (years)	Average carapace length (mm)	
	Male	Female
1	11	11
2	35	35
3	60	60
4	78	78
5	94	90
6	109	98

Bay, is shown to the left in Figure 28. From the first adult form to the end of the first year of life at a length of 11 mm a crab undergoes approximately 11 molts. From the end of the first year to the end of the third year immature crabs molt eight additional times, and thereafter they molt only once a year. For male crabs 80 mm and longer, the growth per molt remains nearly constant. For female crabs growth per molt decreases with increase in size.

Data presented here indicate that the immature stage of the king crab is completed at age 5 in the male and at 5½ years in the female. Growth in the first three years of life is based on Unalaska data, and for the last three years mainly on Bristol Bay data. At the junction of these two growth records (60 mm carapace length) there is a flection. An attempt has been made to explain the existence of this flection on the basis that immature crabs enter the prepubertal phase at this size. It has been demonstrated that changes in allometric growth and growth per molt occur at a length of approximately 60 mm, and one may expect these changes to be expressed in the growth curve. The possibility certainly exists, however, that two different rates of growth are involved. If the growth curve below 60 mm length were extrapolated following the growth trend as depicted by Unalaska crabs, maturity in males would occur at slightly less than five years. Conversely, extrapolation of the growth curve as represented by the growth of males in Bristol Bay would give an estimate of maturity of six years—a difference of approximately one year.

Evidence indicates that growth of king crabs does differ from region to region. Vinogradov (1947) reported that the average weight of male king crabs caught in the Primore district (northern Sea of Japan) is 3.2 kg as compared with an average weight of 1.84 kg for male crabs taken off the west coast of Kamchatka. He stated that such a variation in weight cannot be explained by differences in fishing intensity between the two areas. Wallace *et al.* (1949) wrote that mature male and female king crabs of the southeastern Bering Sea weigh less than Gulf of Alaska crabs of the same carapace length. Also, Gulf of Alaska crabs are noticeably larger than crabs from the southeastern Bering Sea, both in maximum size attained and average size as taken by the fishery. Whether these differences in length and weight are a reflection of growth throughout life is open to conjecture. Kurata (1961 b) believed differences in size between areas to be the result of variations in environmental temperature which affect the growth of crabs throughout their life cycle.

In comparison with other growth curves for immature king crabs (Figure 2), the curve derived in this study most closely approximates that of Powell (1960 a) for Gulf of Alaska crabs. The growth curve for immature king crabs of the southeastern Bering Sea is slightly to the left of Powell's curve except during the first year of life.

SUMMARY

1. The U.S. Fish and Wildlife Service initiated a study in 1958 to determine the growth of immature king crabs of the southeastern Bering Sea. The method of determining growth was based on analysis of the progression of modes in successive length-frequency distributions. Because immature king crabs change habitat with increase in size, data were collected at two different areas within the southeastern Bering Sea. Growth of immature crabs through a length of 60 mm was studied in Iliuliuk Bay of Unalaska Island, Alaska. Growth of crabs longer than 60 mm was measured in samples from the Bristol Bay fishing region.

2. Immature king crabs in the Bristol Bay fishing region were collected by otter trawls in the summers of 1957 through 1961. All crabs taken were measured, shell condition and sex were noted, and males were tagged and released. Immature crabs at Unalaska were sampled at four equally spaced intervals between April 1958 and May 1959. Samples were collected by SCUBA diving. The crabs were measured, sexed, classified into premolt and postmolt groups on the basis of shell condition, and then held in traps to observe increases in length and weight at molting.

3. Peak of hatching in the Bristol Bay region varies from year to year, but most often falls in early May. Peak of hatching at Unalaska takes place in mid-April. Duration of larval life in Bristol Bay was calculated to be three months; the glaucothoe larvae metamorphose into the first adult form by mid-August. Because of the higher water temperature at Unalaska, appearance of the first adult form occurs in early July, or approximately six weeks earlier than in Bristol Bay.

4. Size at maturity was determined by comparison of the proportion of females with and without eggs at

various carapace lengths, and by analyzing changes in length-width relationships. Both male and female king crabs of the southeastern Bering Sea mature at approximately 95 mm, carapace length.

5. Individual characteristics evident in the arrangement of carapace spines made it possible to match correctly cast carapaces with newly molted individuals under both confined and unconfined conditions. The amount of growth per molt for confined crabs 4 mm to 60 mm long ranged from 23 percent at 10 mm to 27 percent at 50 mm. The growth of unconfined crabs 9 mm to 37 mm long was one percent greater. Immature crabs longer than 60 mm show an increase of approximately 16 mm per molt.

6. The length-width ratio for immature king crabs has a flection at approximately 60 mm, carapace length. This flection appears at the size at which immature crabs enter the prepubertal phase of their life cycle.

7. The average length-weight relationship for crabs 9 mm to 50 mm long is expressed by the equation: $W=0.0012\ L^{2.937}$, where W is the body weight in grams and L is the carapace length in millimeters. Approximately 90 percent of the total weight gain for any one molt occurs within one day after molting.

8. The progression of length modes indicates that Unalaska king crabs attain a size of 60 mm, carapace length, at age 3. Separation of each length mode into premolt and postmolt groups and plotting the modes of these groups on their respective sides of the unseparated length modes indicates that the variation in length expected in analysis of progression of modes was plus or minus 15 percent.

9. Analysis of length-frequency distributions of Bristol Bay samples indicates that immature crabs longer than 65 mm molt annually.

10. Combination of data from Unalaska and Bristol Bay gave a growth curve for the entire immature stage. A male king crab hatched in the southeastern Bering Sea in late April reaches maturity five years later. A female king crab hatched at the same time requires 5½ years to attain maturity. The growth curves for the sexes are similar up to the fourth year of life (length of 80 mm). Beyond 80 mm the amount of growth per molt in the female crab decreases, whereas in the male growth per molt remains nearly constant through maturity.

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Appendix Table I. Increase in carapace length at molting for 317 immature king crabs collected at Unalaska in 1958–59.

A. Sampling period 1. N=86
Dates of molting: 4/25–6/6, 1958.

Sex[1]	Carapace length (mm)		Growth increment
	Premolt (L_n)	Postmolt (L_{n+1})	
Un	9.0	11.6	2.6
F	33.0	43.0	10.0
Un	10.0	12.0	2.0
Un	10.0	12.0	2.0
Un	11.0	13.0	2.0
Un	11.0	13.0	2.0
Un*	34.0	44.0	10.0
Un*	9.0	11.0	2.0
Un	10.0	12.0	2.0
F	25.0	31.0	6.0
M	37.0	46.0	9.0
Un	11.0	13.5	2.5
F	34.5	41.5	7.0
M	34.0	43.0	9.0
M	35.0	44.0	9.0
F	28.0	34.0	6.0
M	34.5	43.0	8.5
F	30.0	39.0	9.0
F	35.0	44.0	9.0
Un	33.0	41.0	8.0
F	10.3	12.5	2.2
M	33.5	43.0	9.5
F	34.3	43.3	9.5
Un	11.0	13.0	2.0
M	31.8	40.5	8.7
M	35.8	44.0	8.2
Un	10.3	12.1	1.8
F	34.5	43.5	9.0
F	35.8	44.0	8.2
M	36.0	44.5	9.5
M	33.5	42.5	9.0
Un	10.5	12.5	2.0
F	35.0	44.5	9.5
M	36.0	45.0	9.0
M	33.5	42.0	8.5
F	36.8	46.5	9.7
M	28.0	35.3	7.3
F	37.0	45.5	8.5
M	35.8	42.8	7.0
Un	14.0	16.2	2.2
Un	11.5	14.3	2.8
Un	10.2	13.6	3.4
Un	10.0	12.6	2.6
Un	10.1	12.4	2.3
F	34.5	42.0	7.5
F	42.3	54.0	11.7
F	29.3	37.0	7.7
F	39.2	48.2	9.0
M	34.0	43.0	9.0
F	35.5	43.1	7.6
F	34.5	43.0	8.5
M	35.2	43.5	8.3
F	38.0	47.0	9.0
Un	10.0	12.0	2.0
F	33.3	41.6	8.3
F	31.8	39.5	7.7
F	33.5	41.1	7.6
F	34.0	42.1	8.1
F	36.5	44.0	7.5
F	34.5	42.7	8.2
Un	10.3	13.0	2.7
F	14.7	18.7	4.0
F	13.5	16.5	3.0
F	13.3	17.0	3.7
M	32.5	41.0	8.5
F	35.5	44.6	9.1
M	35.1	44.0	8.9
F	36.6	44.0	7.4
M	29.6	38.0	8.4
F	34.0	42.0	8.0
F	39.0	48.0	9.0
M	12.5	15.1	2.6
Un	9.9	11.5	1.6
F	37.0	46.0	9.0
F	40.0	49.6	9.6
M	35.0	42.5	7.5
F	34.0	42.0	8.0
M	37.5	45.5	8.0
F	38.0	43.0	5.0
M	35.0	42.8	7.8
M	39.0	45.8	6.8
F	36.0	43.3	7.3
Un	13.1	16.0	2.9
Un	9.5	11.5	2.0
F	40.5	50.0	9.5
M	36.0	44.8	8.8

[1] F=female, M=male, Un=sex unknown, * molted prior to collection.

Appendix Table I. Continued.

B. Sampling period 2. N=62
Dates of molting: 9/17–10/1, 1958.

Sex[1]	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment	Sex	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment
F	21.5	28.0	6.5	M	26.0	32.0	6.0
Un	22.0	28.0	6.0	M	22.0	27.2	5.2
Un	18.0	22.5	4.5	M	15.0	18.2	3.2
Un	22.0	28.5	6.5	F	24.7	31.1	6.4
M	20.5	25.3	4.8	M	20.0	25.1	5.1
M	20.5	26.5	6.0	M	22.5	28.3	5.8
M	24.0	29.5	5.5	M	22.3	28.0	5.7
F	21.3	27.5	6.2	F	21.0	26.0	5.0
M*	19.8	25.5	5.7	F	21.3	27.5	6.2
F	19.5	25.0	5.5	M	20.5	26.0	5.5
M	24.0	30.0	6.0	M	20.2	25.0	4.8
M	23.5	29.5	6.0	F	20.7	26.2	5.5
F	25.0	30.3	5.3	M	22.0	27.8	5.8
F	26.0	31.5	5.5	M	21.0	26.5	5.5
M	21.5	27.7	6.2	M	24.0	39.7	6.7
M	23.8	30.2	6.4	F	18.0	23.0	5.0
M	22.5	29.0	6.5	M	22.0	27.2	5.2
M	23.8	29.3	5.5	F	24.5	29.8	5.3
F	23.3	29.7	6.4	F	24.0	30.0	6.0
F	23.0	27.2	4.2	F	19.2	23.5	4.3
M	24.0	29.5	5.5	M	24.0	30.0	6.0
M	17.5	22.5	5.0	M	19.5	24.5	5.0
M	18.5	23.2	4.7	M	20.0	25.8	5.8
M	24.2	30.5	6.3	M	20.3	25.3	5.0
F	23.3	29.2	5.9	F	19.0	24.5	5.5
M	25.2	31.5	6.3	F	19.3	25.3	6.0
M	21.5	25.0	4.5	M	20.3	25.7	5.4
F	23.5	29.5	6.0	F	22.0	27.2	5.2
M	23.2	28.5	5.3	F	25.0	30.5	5.5
M	23.8	29.8	6.0	M	19.2	24.2	5.0
M	19.5	24.0	4.5	Un	4.3	5.1	0.8

APPENDIX TABLE I. Continued.

C. Sampling period 3. N=151
Dates of molting: 2/11-24, 1959.

Sex[1]	Carapace length (mm) Premolt (L_n)	Carapace length (mm) Postmolt (L_{n+1})	Growth increment	Sex	Carapace length (mm) Premolt (L_n)	Carapace length (mm) Postmolt (L_{n+1})	Growth increment
M*	28.0	36.5	8.5	F	39.0	49.6	10.6
F*	29.5	38.8	9.3	F	37.7	49.4	11.7
F*	27.4	36.8	9.4	M	44.5	57.6	13.1
F*	23.5	30.0	6.5	M	37.5	48.2	10.7
M*	26.8	35.2	8.4	F	41.4	53.9	12.5
F	32.0	40.8	8.8	F	37.0	48.3	11.3
F	29.8	38.4	8.6	M	41.4	53.2	11.8
M	30.2	38.6	8.4	M	38.9	50.4	11.5
M	61.8	76.4	14.6	M	32.8	42.4	9.6
M	27.5	34.7	7.2	F	28.9	37.3	8.4
M	39.6	47.0	7.4	M	26.2	33.6	7.4
F	28.3	35.1	6.8	M	27.0	35.8	8.8
M	44.4	56.3	11.9	M	40.7	52.2	11.5
M	37.5	49.0	11.5	M	26.8	36.3	7.7
M	30.0	38.7	8.7	M	40.7	53.3	12.6
F	38.3	48.2	9.9	F	36.5	43.0	6.5
M	45.0	57.5	12.5	F	37.0	44.6	7.6
F	45.5	55.3	9.8	F	37.0	48.2	11.2
F	42.8	55.3	12.5	M	25.3	32.2	6.9
M	37.6	50.5	12.9	M	41.3	53.6	12.3
F	41.5	53.0	11.5	M	8.0	9.8	1.8
F	38.3	48.1	9.8	M	43.3	55.0	11.7
F	43.0	55.0	12.0	F	36.9	48.5	11.6
M	44.2	55.3	11.1	F	39.2	51.8	12.6
F	41.0	53.0	12.0	M	36.6	46.4	9.8
F	42.1	54.2	12.1	F	38.2	50.4	12.2
F	41.2	52.7	11.5	M	41.2	53.1	11.9
F	37.8	47.8	10.0	F	56.7	70.8	14.1
F	43.1	55.8	12.7	M	34.9	46.2	11.3
F	41.5	52.2	10.7	F	35.2	44.8	9.6
M	25.5	33.0	7.5	F	36.0	46.7	10.7
F	43.6	58.5	12.9	M	41.2	51.7	10.5
F	33.8	43.3	9.5	F	36.0	45.8	9.8
F	45.2	55.7	10.5	F	39.8	52.0	12.2
M	43.8	54.2	10.4	F	36.3	47.6	11.3
M	41.6	54.0	12.4	F	38.0	49.0	11.0
M	42.4	55.4	13.0	F	26.8	34.2	7.4
M	44.7	56.7	12.0	M	44.9	58.0	13.1
M	41.0	54.0	13.0	M	38.3	49.4	11.1
F	41.9	54.8	12.9	M	39.1	50.5	11.4
F	43.2	56.0	12.8	M	45.7	57.7	12.0
F	41.4	54.5	13.1	M	30.3	38.8	8.5
F	43.5	55.5	12.0	M	37.2	47.0	9.8
F	42.7	55.5	12.7	M	39.4	50.0	10.6
M	36.8	48.2	11.4	F	45.0	57.7	12.7
F	41.0	52.3	11.3	M	38.2	48.2	10.0
M	41.5	53.0	11.5	M	46.9	59.9	13.0
F	42.2	55.5	13.3				

Continued . . .

APPENDIX TABLE I. Continued.

C. Continued.

Sex[1]	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment
M	23.6	29.3	5.7
M	46.6	57.0	10.4
M	45.9	61.2	15.3
M	7.2	9.3	2.1
F	45.7	58.3	12.6
F	46.9	59.2	12.3
M	44.2	58.0	13.8
F	47.0	61.3	14.3
M	52.6	65.2	12.6
F	38.9	48.4	9.5
F	41.3	53.3	12.0
M	43.1	54.7	11.6
M	41.0	52.0	11.0
M	42.3	55.2	12.9
M	38.0	47.3	9.3
M	38.9	50.1	11.2
M	41.6	54.3	12.7
M	52.2	67.0	14.8
F	37.0	49.7	12.7
M	39.8	51.1	11.3
M	26.1	32.1	6.0
F	26.8	34.3	7.5
M	80.1	97.0	16.9
F	69.2	85.5	16.3
F	42.3	56.0	13.7
F	39.8	51.6	11.8
M	37.2	47.6	10.4
M	26.9	33.7	6.8
F	57.4	73.6	16.2
M	6.5	7.3	0.8
M	73.0	89.2	16.2
M	36.8	45.8	9.0
M	38.2	48.3	10.1
F	37.8	49.6	11.8
M	44.2	58.0	13.8
F	43.2	54.6	11.4
M	39.1	49.1	10.0
M	39.9	50.8	10.9
F	52.0	67.3	15.3
M	42.2	53.8	11.6
F	43.8	55.0	11.2
M	50.6	63.8	13.2
M	41.1	53.3	12.2
F	48.0	61.3	13.3
M	49.7	61.9	12.2
M	53.4	64.9	11.5
M	7.1	8.6	1.5
F	6.4	7.9	1.5
M	60.3	74.1	13.8
F	62.2	79.8	17.6
F	43.5	56.6	13.1
M	37.7	49.3	11.6
F	40.5	53.2	12.7
M	38.9	49.4	10.5
M	39.7	52.8	13.1
M	40.5	53.2	12.7

D. Sampling period 4. N=18
Dates of molting: 5/25-6/2, 1959.

Sex[1]	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment
F*	32.2	41.4	9.2
F*	36.8	48.1	11.3
F*	36.2	46.0	9.8
F	34.0	42.3	8.3
F	35.0	44.8	9.3
M*	29.2	36.3	7.1
M	33.3	41.5	8.2
M	27.7	35.5	7.8
M	26.3	32.0	5.7
M	9.4	11.4	2.0
F	9.7	12.5	2.8
F	28.3	36.1	7.8
F	29.7	38.1	8.4
M	29.1	36.3	7.2
F	34.4	44.4	10.0
F	33.5	42.2	8.7
F	27.0	33.2	6.2
F	38.3	46.7	8.4

Appendix Table II. Length-frequency distributions by sampling period, area of capture, and molting stage of king crabs collected in the vicinity of Unalaska in 1958–59.

	1						2			3									4					
Sampling period	4/22–5/17				5/30–6/6	7/13	9/17–10/1			2/11–2/24									5/24–6/2					
Area sampled[1]	1	2	*	Total	2	2	2	4	Total	1		2		3		4		Total	2		4		*	Total
Molting stage	not recorded									pre	post	pre	post	pre	post	pre	post		pre	post	pre	post		
Carapace length (mm)																								
4							5		5															
5							9		9															
6							2		2															
7												4	4					8						
8		3		3								1	10					11	1					1
9		11	1	12	1								5					5	2					2
10		33		33	3								3					3	4	5				9
11		24	1	25	9														1	13			4	18
12		35	1	36	26															14			3	17
13		76	3	79	26	2														4				4
14		62		62	13															2				2
15		27		27	6	4	2		2														1	1
16		2		2		3	4		4											1				1
17		2		2	1	3	3	4	7															
18					1	4	12	3	15														1	1
19		1		1			21	7	28															
20							31	4	35															
21		1		1			33		33															
22			1	1			31	1	32							1		1						
23		1		1			40		40			1				1		2			1			1
24		2		2			28	1	29			2				1		3			1			1
25		1	1	2			22		22			5	1					6			1			1
26		3	1	4			28		28			6	1					7	1		3			4
27		5		5			29	1	30			10	3			1	2	16			6			6
28		2		2			18	1	19			6	1				4	11		1	6	3		10
29	1	2		3	2		16	1	17			7	4		1	1	6	19		1	5	1		7
30	5	7	1	13	2		12		12			9	7			1	1	18		1	8	11		20
31	2	10	1	13	2		11		11			3	9				3	15	2	3	4	14		23
32	6	23		29	1		11		11			6	13				3	22	2	3	1	15		21
33	1	17		18	3		3		3	2			9				2	13	4	4	1	11		20
34	4	24		28	7		2		2	4		2	10				2	18	4	4	2	18		28
35	1	33		34	6					8		1	17					26	6	6	1	10	1	24
36		44		44	6					22	1		16				1	40	4	11	1	7		23
37		34		34	14					52		1	15					68	4	16		9		29
38		35		35	9			1	1	54			17			1	1	73	3	16		7		26
39		31		31	21					60			7			1		68	2	14		4	1	21
40		28		28	18					72			4				1	77		21		1	1	23
41		12		12	13	1		1	1	74	2	1	5					82	1	12		2		15
42		16		16	7			1	1	50	2		3	4				59		18				18
43		8		8	6					50	2		2	8		2		64		9				9
44		10		10	5			4	4	36	1	1	2	11		1	1	53		14				14
45					10			3	3	27	3			12		4		46		6				6
46		6		6	6			3	3	32	6	1		15		6		60		6				6
47		2		2	1			4	4	14	10	1		16		6		47		2				2
48		4		4	3					4	12			22		2	1	41		4				4
49					3			1	1	1	15			28		2	2	48						

Continued . . .

Appendix Table II. Continued.

	1						2			3									4					
Sampling period	4/22–5/17				5/30 –6/6	7/13	9/17–10/1			2/11–2/24									5/24–6/2					
Area sampled[1]	1	2	*	Total	2	2	2	4	Total	1		2		3		4		Total	2		4		*	Total
Molting stage	not recorded									pre	post	pre	post	pre	post	pre	post		pre	post	pre	post		
Carapace length (mm)																								
50					2						23			27		4		54		2				2
51										3	24			28	1			56		1				1
52								1	1		12			16		1	1	30						
53								1	1		10			23	2	1		36						
54											11			13		1		25						
55											10			10	1	1		22						
56					1						7			13	1	3		24						
57											5			10	3	5		23						
58										1	3			4	1	5		14						
59											3			5	3	4	2	17						
60		1		1							3			9	2	8		22						
61											2			12	4	5		23						
62										1				9	5	7		22						
63														10	10	5		25						
64											3			5	1	3		12						
65											1			6	3	3	1	14						
66											1			3	2	1		7						
67											2			1	3	2		8						
68														1	1	2		4						
69											1			1	3	3		8						
70														2		1		3						
71		1		1																				
72														1	1	1		3						
73															2			2						
74											1			1	1		1	4						
75			1	1											1			1						
76											1							1				1		1
77															1		1	2						
78															6	1		7						
79															2			2						
80															2			2						
81																								
82															2			2						
83																								
84																								
85																								
86																								
87																								
88																								
89											1				1			2						
90																								
91											1							1						
Total	20	639	12	671	234	17	373	43	416	567	179	68	168	326	66	98	36	1,508	41	214	41	114	12	422

[1] See Figure 3. * indicates crabs were collected in areas other than 1, 2, 3, and 4.