

CONTRIBUTION TO THE LIFE HISTORY OF THE DEEP-SEA KING CRAB, *LITHODES COUESI*, IN THE GULF OF ALASKA¹

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ABSTRACT

Lithodes couesi is a deepwater relative of the commercially important Alaskan king crabs, *Paralithodes camtschatica*, *P. platypus*, and *L. aequispina*. Compared with the *Paralithodes* species, which are primarily restricted to the continental shelf, *L. couesi* displays a variety of features which appear to be adaptations for life in deeper water on the continental slope, including elongated legs, red coloration, inflated branchial chambers, asynchronous spawning, and large eggs. Fecundity of *L. couesi* increases asymptotically with carapace length according to the relationship $E = 4,329 - 3.19 \times 10^9 e^{-0.172L}$. The size of 50% maturity is reached at 91.4 mm for males and at 80.2 mm for females.

The deep-sea king crab, *Lithodes couesi*, is a little known relative of the three species of king crab, *Paralithodes camtschatica*, *P. platypus*, and *L. aequispina*, commercially harvested in Alaska. Since its original description (Benedict 1895), *L. couesi* has been discussed only in taxonomic works (Rathbun 1904; Schmitt 1921; Makarov 1938; Sakai 1971); other than its geographical distribution (San Diego, Calif., to Onohama, Japan) and depths of occurrence (542-1,125 m), nothing has been reported concerning the life history of this species.

Considering its rather large size and conspicuous bright red color, it is surprising that *L. couesi* has not received more attention. One reason for this is that benthic sampling surveys infrequently reach the depths inhabited by *L. couesi*, and those that do typically are not designed to catch a large number of specimens. However, in 1979 a National Marine Fisheries Service (NMFS) cruise surveying the commercial fishing potential of seamounts in the Gulf of Alaska caught nearly 1,500 *L. couesi* in large baited traps. The present study is based on these specimens.

Although *L. couesi* is unlikely soon to become the target of a commercial fishery due to the great depths it inhabits, the high value of crab and the fluctuating supply of other Alaskan crab species may stimulate technological developments making deepwater crab fishing more economical. Such developments have already occurred in the fishery

for another deepwater crab, *Geryon quinquedens*, along the east coast of North America (Wigley et al. 1975). This paper is intended to provide a comparison of life history characteristics between *L. couesi* and shallow-water king crabs, as well as to provide some information needed by fisheries managers in the event *L. couesi* were to become commercially important.

METHODS

Samples of *L. couesi* were collected between 31 May and 5 July 1979 on an NMFS stock assessment cruise to eight seamounts located in the central Gulf of Alaska (Figure 1). All specimens except three were captured in baited traps. Three types of trap were used: rectangular sablefish, *Anoplopoma fimbria*, traps measuring 0.8 m × 0.8 m × 2.5 m and covered with 8.9 cm (bar measure) webbing; conical sablefish traps measuring 0.7 m high × 1.2 m base diameter × 0.9 m top diameter and covered with 7.5 cm webbing; and rectangular king crab traps measuring 1.8 m × 1.8 m × 0.6 m and covered with 11.4 cm webbing. Traps were arranged at 91.5 m intervals along a 1,006.5 m groundline having surface floats connected to both ends. A typical set of gear included four or five of each type of sablefish traps, plus two king crab traps in 8 of the 25 sets. A total of 232 traps (102 conical, 114 rectangular, 16 king crab) were set. Three small specimens of *L. couesi* were obtained in one haul of a bottom trawl.

All seamounts were extremely steep sided, rising approximately 3,000 m from the seafloor to relatively flat summits composed of rock outcrops

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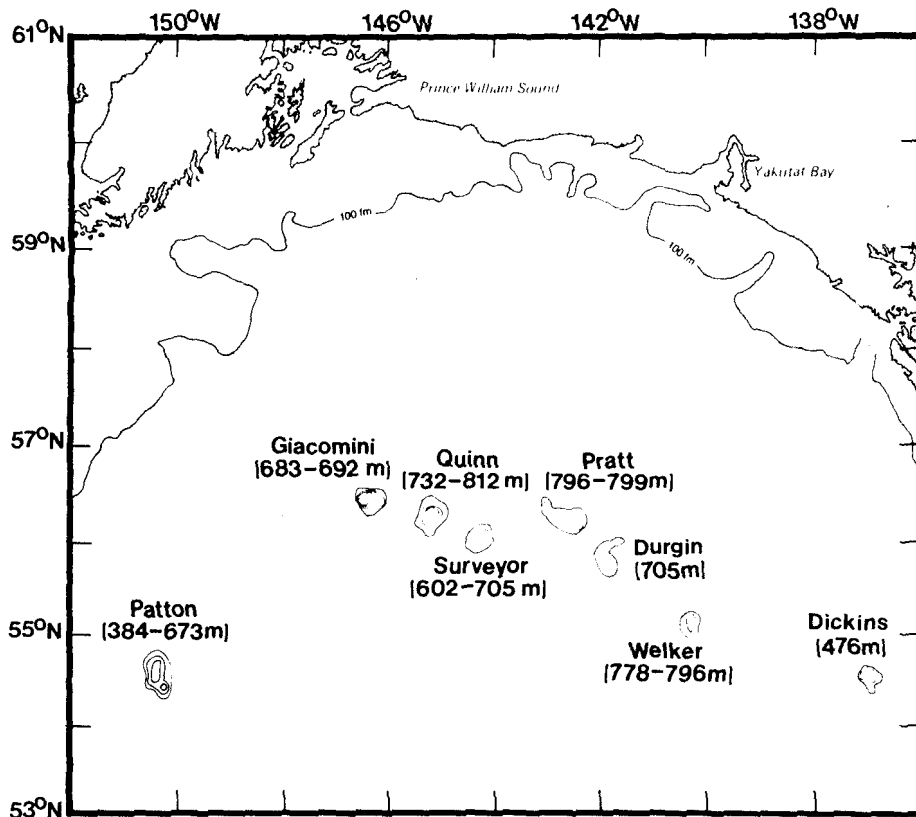


FIGURE 1.—Location of the eight seamounts which were surveyed on a 1979 NMFS cruise to the Gulf of Alaska. The range of sampling depths on each seamount is indicated.

with intervening sediments. This physiography limited sampling to the seamount tops. Sampling depths ranged from 384 m on the Patton Seamount to 850 m on the Quinn Seamount.

The carapace lengths of all crabs and the right chela heights of males were measured to the nearest 0.1 mm using vernier calipers (see Wallace et al. (1949) for a description of these two measurements). The reproductive condition of females was scored according to the following six-point scale:

- 1) Immature—white undeveloped ovaries and no egg remnants on the pleopod bristles.
- 2) Virgin—orange developed ovaries and no egg remnants on the pleopod bristles.
- 3) New eggs—orange external eggs with no evidence of embryonic eyes.
- 4) Developing eggs—tan external eggs with obvious dark embryonic eyes.
- 5) Hatching eggs—partial clutch of well-developed eggs, with remnants of hatched

eggs attached to pleopod bristles and occasionally with prezoaea on the egg mass.

- 6) Completely hatched—no external eggs, but remnants of eggs, especially the egg funiculi, attached to the pleopod bristles.

Abdomens, complete with attached eggs, were removed from a selected number of females and preserved in buffered 10% Formalin.³ In the laboratory, the pleopods from females with new and developing eggs were removed and dried. After freeing the eggs from the pleopods, the total clutch was weighed and a subsample was weighed and counted. Total egg number was calculated by dividing total clutch weight by the average egg weight of the subsample. Maximum egg length was measured to 0.1 mm using an ocular micrometer. Measured eggs were well developed and

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

apparently close to hatching, and had been stored in 33% isopropyl alcohol after being fixed in Formalin.

RESULTS AND DISCUSSION

Depth Distribution

Specimens of *L. couesi* were collected in every trap set from the shallowest in 384 m to the deepest in 850 m. Four sets on two seamounts were at depths less than the depth range (542-1,125 m) previously recorded for this species (Sakai 1971).

Lithodes couesi occurs shallower on seamounts than on the continental slope. This hypothesis is supported by the results of a concurrent NMFS survey of the southeast Alaska continental slope that sampled roughly the same latitudes (54°-58° N) and depths (237-711 m) and used the same types of traps as the seamount study. Although depths <550 m were thoroughly sampled, specimens of *L. couesi* were not taken in <592 m (H. Zenger⁴).

The shallow distribution of *L. couesi* on seamounts may be due to the absence of a predator or competitor which is able to exclude it from similar depths along the continental slope. Because seamounts are isolated from the ocean surface and from coastal areas, they are essentially submarine islands inhabited only by species that are able to tolerate the available depth range and that possess sufficient dispersal capabilities to reach seamounts from the continental slope. If a predator or competitor were unable to colonize the seamounts, *L. couesi* may respond by expanding its range into shallower water. A similar pattern of competitive release and altitudinal expansion has been reported for birds on South Pacific islands (Diamond 1975).

Size Distribution

The size distribution of each sex was nearly unimodal with a mode at about 108 mm for males and 92 mm for females (Figure 2). The lack of an appreciable number of crabs <70 mm is probably due to size selectivity of the sampling gear, rather than a lack of small crabs on the seamount tops, because three of the four smallest specimens were caught with a bottom trawl in an area of the

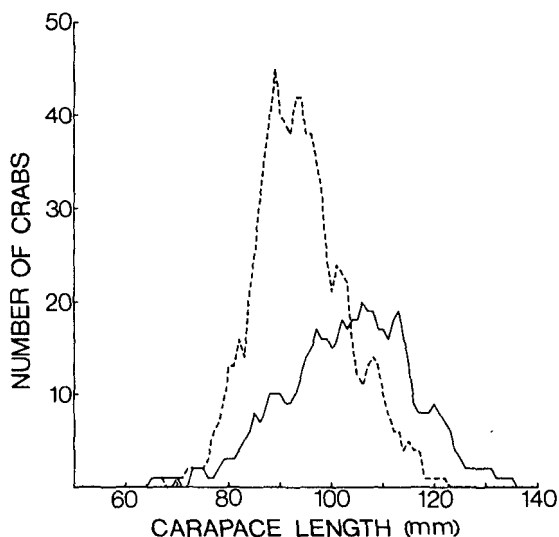


FIGURE 2.—Size distribution of male (solid line) and female (dotted line) *Lithodes couesi* by 2 mm size intervals from trap samples from Gulf of Alaska seamounts.

Patton Seamount where only larger crabs were obtained with traps.

Other species of king crabs, especially *P. camtschatica* and *P. platypus*, display size stratification with depth; adults generally occur deeper than juveniles (pers. obs.). To determine if *L. couesi* also stratify, crab size was regressed against depth. Only the sizes of crabs from sablefish traps were used in the regression because king crab traps caught significantly larger crabs than sablefish traps when both types were fished together (*t*-test, $P < 0.001$) and because king crab traps were not used on every seamount. For males, the slope of the regression line was not significant ($P = 0.289$). For females, the slope was significant ($P = 0.030$) and negative, indicating that larger females occur in shallow water. However, there was little variation in sampling depth on each seamount; thus, size variation with depth cannot be separated from size variation between seamounts.

Sex Ratio

In total, 880 females and 577 males were captured in 24 trap sets. The large preponderance of females suggested that the sex ratio may not be 1:1. If the sex of each specimen were independent of the sex of other specimens in the same set, then the observed proportion male, 0.40, is signifi-

⁴H. Zenger, Fishery Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. commun. June 1980.

cantly different than 0.50 ($Z = 7.8, P \leq 0.001$). Sex ratio, however, was not homogenous between trap sets ($\chi^2 = 137.5, P \leq 0.0001$), indicating that the sex of each specimen was not independent of other specimens but highly correlated. Thus, females tended to be caught with other females and males tended to be caught with other males. Segregation by sex is also commonly observed for *P. camtschatica* (pers. obs.).

Although the sexes of crabs within each set are correlated, the hypothesis of a 0.50 proportion male in the population can still be tested if each set is assumed to be an independent random sample. The test is made by calculating a *t*-statistic from the mean and variance of the proportion male within individual trap sets. Because the number of crabs within each set varied considerably, the mean proportion was calculated as a weighted average, with the weighting factors equal to the number of crabs in each set (Cochran 1943). The *t*-test was not significant ($t = 0.396, P = 0.86$); thus, a 1:1 sex ratio is not rejected.

Female Reproductive Condition

The number of female *L. couesi* in each of the six categories of reproductive condition is shown as a function of size in Figure 3. Eighty-six percent of the females examined were mature (categories 3-6). Virgin females had partially developed ovaries and appeared to have never spawned previously. Assuming virgin female *L. couesi* require the same length of time to complete maturity as "pubescent" female *P. camtschatica* (Powell et al. 1973), their first spawning will occur soon after their next molt in the following spring.

Mature female *L. couesi* display more heterogeneity in their reproductive condition than female *P. camtschatica*. This is exemplified in the following table, where the percentage of mature female *L. couesi* in each of the four mature reproductive categories is compared with the equivalent reproductive categories of female *P. camtschatica* collected in the eastern Bering Sea at the same time as the seamount survey.

Species	Devel-		Completely	
	New eggs	oping eggs	Hatching eggs	hatched eggs
<i>L. couesi</i>	50	35	6	9
<i>P. camtschatica</i>	97	2.....	1

Although no distinction was made between devel-

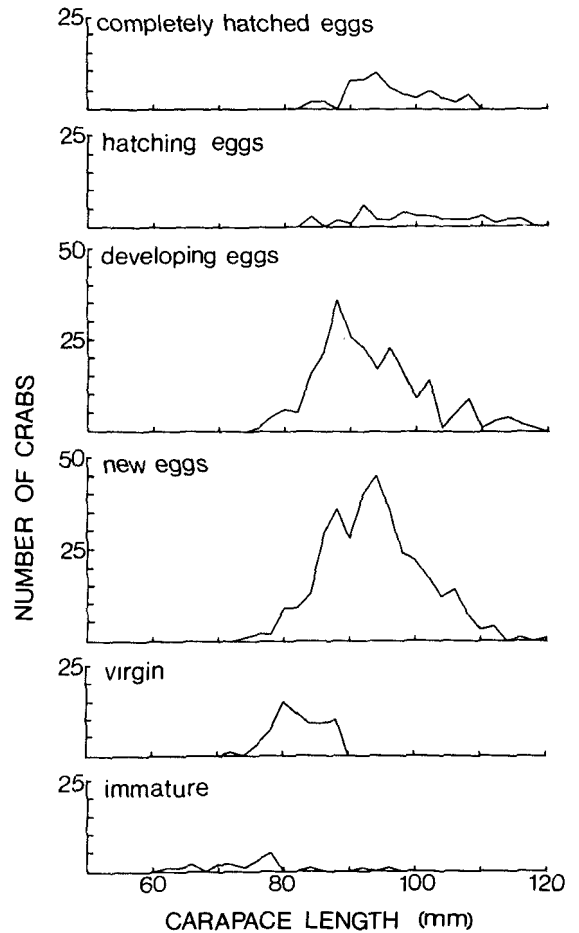


FIGURE 3.—Number of female *Lithodes couesi* by 2 mm size intervals in each of the six categories of reproductive condition described in the text.

oping and hatching eggs for *P. camtschatica*, it is evident that *P. camtschatica* had nearly completed spawning and were carrying new eggs, whereas *L. couesi* had not completed spawning and were carrying eggs in a variety of developmental stages.

If *L. couesi* are similar to *P. camtschatica* in spawning soon after hatching the previous clutch, then the heterogeneity in their reproductive condition can be interpreted in either of two ways. First, *L. couesi* were sampled midway in their spawning season; therefore, the maturing eggs hatch later in the season. Second, *L. couesi* were sampled at the end of the spawning season; therefore, the maturing eggs are from spawning in the current season and hatch in the succeeding year. The difference in these interpretations

reflects the degree of reproductive synchrony in the population. If the first interpretation were correct, *L. couesi* could be as synchronized as *P. camtschatica* and the heterogeneity in reproductive condition could merely be due to fortuitous timing of the survey. But if the second interpretation were correct, *L. couesi* would be quite asynchronous compared with *P. camtschatica* because, at least in *P. camtschatica*, the eyed (developing) eyes would have been spawned at least 4 mo previous to sampling (G. C. Powell⁵). Although the embryological development of *L. couesi* eggs was not studied—this would be necessary to completely resolve the question—I believe that the second interpretation, that *L. couesi* has an asynchronous spawning, is correct because the eggs classified as developing were clearly in a much earlier stage of development than were the hatching eggs.

The asynchronous spawning of *L. couesi* is probably related to the great depths which it inhabits. Temperate species having planktotrophic larvae typically have synchronous breeding cycles because of the rather brief periods which are optimum for larval survival. Since seasonal fluctuations are damped with depth, *L. couesi* may be unable to detect seasonal cues with precision, or more likely, may have larvae which do not rise to the euphotic zone and do not need to be synchronized with the surface production cycle. Asynchronous spawning was also observed for another deepwater crab, *Geryon quinquedens* (Haefner 1978). Crustaceans living at depths greater than *L. couesi* have such asynchrony in spawning that seasonal peaks in spawning activity are absent (Rokop 1977).

Size of Maturity

Maturity of females was determined by the presence of eggs or egg remnants on the pleopods. Thus, reproductive categories 1 and 2 were considered immature and categories 3 to 6 were considered mature. Maturity of males was determined from the size of the chela relative to the size of the carapace using a method discussed in Somerton (1980). This method assumes that when chela and carapace measurements are plotted against each other on a double logarithmic scale,

the points lie along two straight lines, one describing the relative growth for juveniles, the other describing the relative growth for adults. A computer technique was used to iteratively fit two lines to the data until the best fit (minimal residual sum of squares) was achieved (Figure 4). Maturity was then based on the final assignment to one of the two categories.

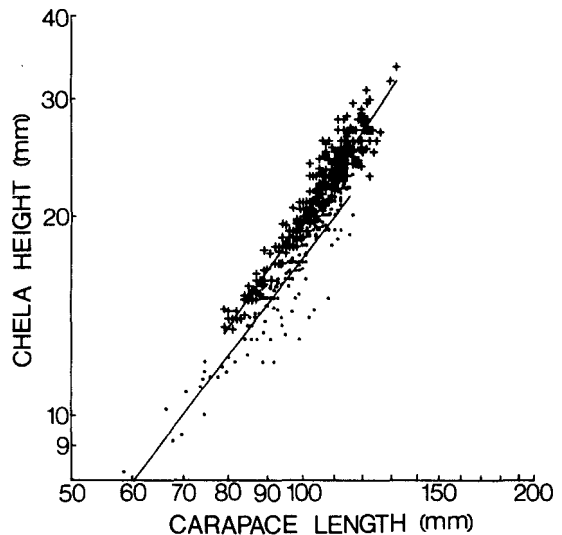


FIGURE 4.—Classification of male *Lithodes couesi* chela height and carapace length measurements into juvenile (dots) and adult (pluses) categories. The relative growth of the chela is described for juveniles by the lower line ($CH = 1.52 CL - 4.17$; SD for intercept and slope are 0.19 and 0.04) and for adults by the upper line ($CH = 1.70 CL - 4.83$; SD for intercept and slope are 0.13 and 0.03). Regression methods of Somerton (1980), see text.

The size of 50% maturity was estimated by fitting a logistic equation to the percentage mature by size using the methods discussed in Somerton (1980), then evaluating the fitted equation to determine the size corresponding to 50% mature. Percentage mature and the fitted logistic equation are shown for both sexes in Figure 5. Estimated sizes of 50% maturity were 91.4 mm for males and 80.2 mm for females.

Fecundity

Fecundity of *L. couesi* increases up to a size of 95 mm and remains fairly constant thereafter (Figure 6). The apparent curvilinear relationship between fecundity and size is similar to that reported for *P. platypus* (Sasakawa 1975) but unlike the strict linear relationships reported for

⁵G. C. Powell, Fishery Biologist, Alaska Department of Fish and Game, Division of Commercial Fisheries, P.O. Box 686, Kodiak, AK 99615, pers. commun. June 1980.

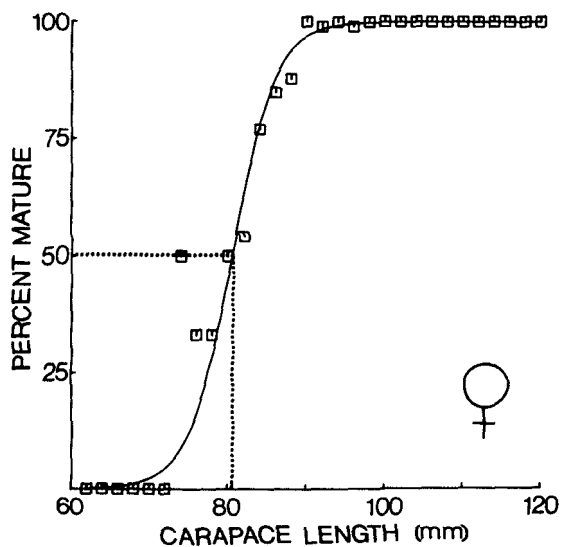
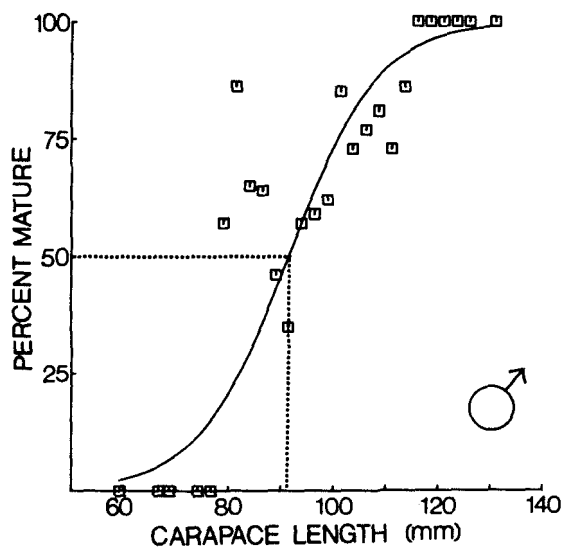


FIGURE 5.—Percentage of male (upper) and female (lower) *Lithodes couesi* classified adult as a function of size. The size of 50% maturity was estimated by first fitting a logistic equation to the data, then determining the size (shown by dotted lines) corresponding to 50% mature.

P. camtschatica (Haynes 1968), *L. aequispina* (Hiramoto and Sato 1970), and *L. antarctica* (Guzman and Campodonico 1972).

An attempt was made to develop an appropriate functional relationship to describe the fecundity and size of *L. couesi*. To determine whether or not this relationship should be curvilinear, the fit of a second degree polynomial was statistically compared with that of a straight line. The coefficient of

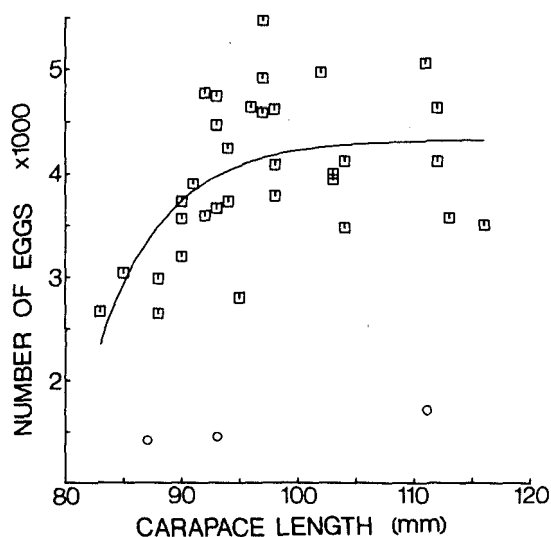


FIGURE 6.—Fecundity of *Lithodes couesi* as a function of size. An asymptotic curve was fit to the data using methods described in the text. Three specimens (shown by circles) had conspicuously fewer eggs. Although these females did not appear to be damaged, their fecundities were excluded from the analysis.

the squared term of the polynomial was highly significant ($F = 12.23$, $P < 0.001$), indicating that the polynomial fit the data better than a straight line; however, a second degree polynomial was not a good relationship because the predicted fecundity did not increase monotonically with size. Since it is unlikely that fecundity reaches some maximum and then diminishes with size, an asymptotic curvilinear relationship was considered. The chosen equation is $E = E_{\infty} - Ae^{-BL}$, where E is egg number, L is carapace length, E_{∞} is a parameter representing the theoretical maximum number of eggs that can be carried, and A and B are parameters controlling the rate at which the maximum egg number is achieved. Using nonlinear regression, the best fit was obtained when $E = 4,329 - 3.19 \times 10^9 e^{-0.172L}$ (Figure 6).

If the number of eggs a female could carry were limited either by the length of the pleopods or by the volume of the brood chamber enclosed between the abdomen and the sternum, then fecundity should increase in proportion to the carapace length raised to a power of one or greater, that is, fecundity should be an upwards concave function of size. The best fitting equation is concave downwards, which indicates that some other mechanism limits fecundity in *L. couesi*. One possible explanation is that the low oxygen con-

centrations at the depth inhabited by *L. couesi* reduce the ability of females to aerate clutches larger than some fixed size.

One consequence of an asymptotic form to the fecundity and size relationship is that the reproductive effort, or the proportion of the total energy intake devoted to reproduction, must decrease over some part of the reproductive lifespan of *L. couesi*. Theory predicts and many animals display an increase in reproductive effort with age (Pianka and Parker 1975). Since fecundity appears to be fairly constant over approximately one-half of the mature size range of *L. couesi*, reproductive effort could increase only if either egg size increased with age or growth ceased. Individual dried egg weight, however, does not increase with crab size ($P = 0.15$), and the lack of wear and accumulation of epifauna on the exoskeleton suggests that molting, and presumably growth, continues throughout the life of females.

Egg Size

Lithodes couesi eggs in a late stage of development have a mean length of 2.3 mm (SD = 0.076, $N = 33$). This size is quite similar to previous estimates of mean or median egg size reported for other species in the genus *Lithodes*—*L. antarctica*, 2.2 mm (Guzman and Campodonico 1972); *L. aequispina*, 2.1 mm (Hiramoto and Sato 1970)—but roughly twice the egg size reported for species in the genus *Paralithodes*—*P. camtschatica*, 1.0 mm (Haynes 1968); *P. platypus*, 1.2 mm (Sasakawa 1975).

The larger size of *Lithodes* spp. eggs compared with *Paralithodes* spp. eggs conforms to a theory of egg size and pattern of larvae development first discussed by Thorson (1950), which proposes that benthic invertebrates generally have large eggs and lecithotrophic larvae in high latitudes or in deep water, but have small eggs and planktotrophic larvae in other areas. At great depths or at high latitudes water temperatures are low and larval development is protracted. Species may compensate for slow larval development by producing larger and more yolky eggs, which in turn result in larger larvae with greater energy reserves. These larval features may be necessary to allow the larvae either to migrate to the surface, to capture a broader array of food items, or to forgo feeding entirely. Stage 1 zoeae of *L. couesi* have conspicuously more yolk than *P. camtschatica* larvae in the same stage of development (J.

Bowerman⁶), but it is unclear whether or not these larvae migrate to the surface. Unusually large eggs have been previously reported for abyssal shrimp (Zarenkov 1965) and abyssal crabs (Garth and Haig 1971).

Parasites

Of the 674 female *L. couesi* examined, 5 were parasitized by the rhizocephalan, *Briarosaccus callosus*. All five females were >90 mm and, on the basis of size alone, should have been mature, but none were carrying eggs and all had unusually small pleopods compared with uninfected crabs of similar size. Thus, similar to other species of crabs (Barnes 1974), *L. couesi* females are apparently castrated by *B. callosus*. One male *L. couesi* was also observed with the parasite; however, the abdomens of males were not routinely examined and other parasitized males could have been missed. *Briarosaccus callosus* has been previously reported as a parasite of *L. couesi* (Boschma 1970).

Adaptations for Life on the Upper Slope

Lithodes couesi is conspicuously different in appearance (Figure 7) from the shallow-water king crabs, *P. camtschatica* and *P. platypus*, because of three features: 1) bright red, 2) inflated branchial chambers, 3) elongated legs. All of these features are apparently adaptations for living in deeper water.

The red coloration of deepwater crustaceans has long been a subject for speculation, but the general consensus is that within some range of depth, red is cryptic due to the rapid attenuation of red light originating from the surface and the low in situ production of red light from bioluminescence (Marshall 1954). At depths greater than this range, the ambient light is too weak for visual predators and crustaceans are often white or transparent (Zenkevich and Birstein 1956); at depths shallower than this range, red may be too conspicuous to visual predators and the red carotenoid pigments are often complexed with proteins to produce blue, green, and brown pigments (Goodwin 1960).

Crabs living on the continental slope have branchial chambers which are more inflated than

⁶J. Bowerman, Fishery Biologist, Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615, pers. commun. June 1980.

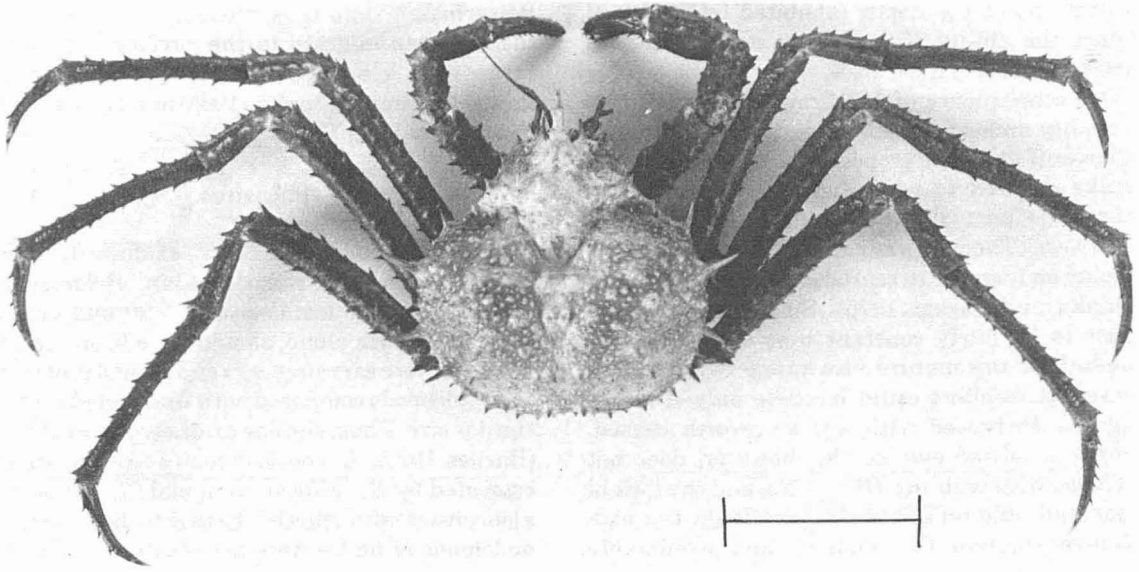


FIGURE 7.—A male specimen of *Lithodes couesi* (a 100 mm bar is included for scale). Generally, *L. couesi* are bright red with the carapace being somewhat lighter than the legs; however, occasional specimens will be light pink. Great variability was found in the length of the spines along the lateral margins of the carapace. The above specimen has especially long spines.

those of crabs living on the shelf. The degree of branchial inflation was quantified by Takeshita et al. (1978) for three anomuran crabs in the family Lithodidae—*P. camtschatica*, *L. aequispina*, *Paralomis verrilli*—and four brachyuran crabs in the genus *Chionoecetes*—*C. bairdi*, *C. opilio*, *C. japonicus*, *C. tanneri*—using moiré photography. For both the anomuran and brachyuran crabs, the branchial chambers were more inflated in the species living at greater depths. In the present study, a similar type of assessment was not made for *L. couesi* due to a lack of suitable photographic equipment; however, the inflation of the branchial chambers appears to be greater than *L. aequispina* (a shallower species) and less than *P. verrilli* (a deeper species). Although I lack data to demonstrate that enlarged gills are associated with inflated branchial chambers, Rathbun (1893), in the original description of *C. tanneri* (a deep species), remarked that "The carapace is much swollen at the branchial regions" compared with *C. opilio* (a shallower species) and that the gills of *C. tanneri* are about two-fifths longer than the gills of an equal-sized specimen of *C. opilio*.

The inflation of crab branchial chambers with increasing depth is related to the distribution of oxygen in the sea. Typically, the concentration of dissolved oxygen decreases with depth until an

oxygen minimum zone is reached, then increases thereafter. In the region of the Gulf of Alaska near the major seamounts, a minimum oxygen concentration of 0.5 ml/l, roughly 7% of the surface concentration, occurs at 1,000 m (Favorite et al. 1976). Since the combined depth ranges of the species considered by Takeshita et al. (1978) extend from 1,400 m to the intertidal, the deeper these species occur, the lower the oxygen concentrations they must deal with. Inflated branchial chambers or unusually large gills have been reported for a brachyuran crab, *Lophorochinia parabranchia* (Garth and Haig 1971), and a mysid, *Gnathophausia ingens* (Childress 1971a), both of which are primarily restricted to oxygen minimum zones.

Lithodes couesi has two additional morphological features allowing respiration in low oxygen concentrations: large exhalent openings and large scaphognathites (appendages located in the exhalent openings and used for pumping water over the gills). Enlargement of these features, compared with related shallow-water lithodid crabs, implies that a relatively greater volume of water is pumped over the gills. *Gnathophausia ingens* was also found to have a large ventilation volume compared with related shallow-water species (Childress 1971a).

To demonstrate that walking legs are more elongated for crab species inhabiting greater depths, two leg dimensions, merus length and propodus length, were compared between deep and shallow species (Table 1). Two trends in

TABLE 1.—Merus height (MH) and propodus length (PL) of the right first walking leg, expressed as a fraction of merus length (ML), are shown for one adult male specimen of three species in the family Lithodidae and three species in the genus *Chionoecetes*. Under each taxonomic section, species are arranged according to depth, with the shallowest species at the top, except for *C. bairdi* and *C. opilio*, which occur at similar depths.

Species	MH/ML	PL/ML
Anomura:		
<i>Paralithodes platypus</i>	0.286	0.715
<i>Lithodes aequispina</i>	.255	.823
<i>L. couesi</i> *	.189	.882
Brachyura:		
<i>Chionoecetes opilio</i>	.222	.576
<i>C. bairdi</i>	.209	.487
<i>C. tanneri</i>	.158	.655

relative leg dimensions are evident. First, the legs become thinner with depth; that is, merus height to merus length decreases. Second, the distal portion of the legs becomes relatively longer with depth; that is, propodus length to merus length increases.

The selective advantage of long slender legs for deepwater crabs is not obvious. Barnes (1974) suggested that: "Many abyssal crabs have long slender legs for crawling about over soft bottoms." Presumably, this means that the propodi and the dactyli are placed flat on the substrate and used, like snowshoes, to spread the body weight more evenly. However, underwater photographs of both *L. couesi* (Figure 8) and *Geryon quinquedens* (see Wigley et al. 1975, fig. 4) show individuals walking over apparently soft bottoms on the tips of the dactyli. An alternative explanation, suggested by Childress (1971b), is that reduced musculature in

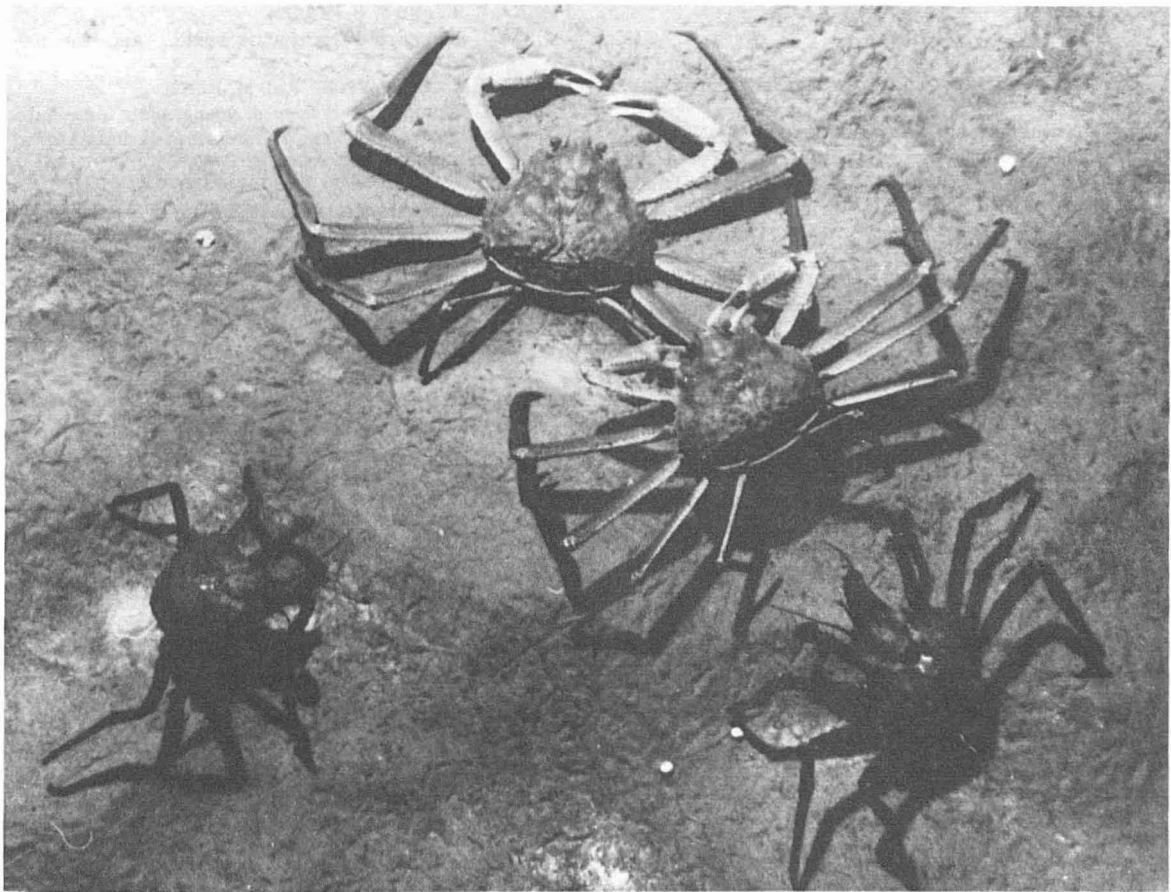


FIGURE 8.—Photograph on the Patton Seamount (500 m) of *Lithodes couesi* (lower) and *Chionoecetes tanneri* (upper) walking across a soft bottom on the tips of their dactyli (photograph taken by P. Raymore).

deepwater crustaceans requires less energy to maintain and thus represents an adaptation for energetic efficiency in a habitat where food is scarce. In addition, long legs may allow a crab to move more rapidly or more economically by taking fewer, larger steps to travel a given distance.

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