Abstract.–Populations of the grooved Tanner crab, *Chionoecetes tanneri*, and the triangle Tanner crab, *C. angulatus*, were surveyed along the continental slope of the eastern Bering Sea with a bottom trawl. Over the depth range sampled (100–1,000 m), the relative abundance of the two species was about equal. Mature male and female *C. tanneri* occurred at the same depths, but for *C. angulatus*, males were found at significantly shallower depths than were females. Carapace widths at 50% maturity for males and females were 118.7 mm and 79.2 mm for *C. tanneri* and 91.4 mm and 57.8 mm for *C. angulatus*. Fecundity of *C. tanneri* did not increase with carapace width (CW, mm) and averaged 86,500 eggs over the sizes sampled. Fecundity of *C. angulatus* increased with carapace width according to the following formula: eggs = –65,600 + 1660 × *CW*. Mean egg diameter was 0.75 mm for *C. tanneri* and 0.74 mm for *C. angulatus*. The relationship between body weight (gm) and carapace width did not differ between species: weight = 1.219 /10^4 × $CW^{3.183}$.

Contribution to the biology of the grooved and triangle Tanner crabs, *Chionoecetes tanneri* and *C. angulatus*, in the eastern Bering Sea

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The continental slope of the North Pacific Ocean is inhabited by several species of crabs in the genus *Chionoecetes* that are similar in size to their shallower, commercially harvested relatives *C. bairdi* and *C. opilio* but are immediately distinguishable by their brilliant orange or red color and slender legs. In the eastern North Pacific Ocean there are two species: the grooved Tanner crab, *C. tanneri*, ranging from northern Mexico to Kamchatka, and the triangle Tanner crab, *C. angulatus*, ranging from Oregon to the Sea of Okhotsk (Hart, 1982). In the western North Pacific there is a single species, *C. japonicus*, which occurs in the Sea of Japan (Sinoda, 1982). Although the potential for commercial fisheries for *C. tanneri* has been recognized for quite some time (Pereyra, 1967), commercially successful fishing ventures have occurred only recently (Jamieson, 1990). In contrast, *C. japonicus* has been commercially fished since the mid-1960's (Sinoda, 1982). The primary impediment to the development of commercial fisheries for *C. tanneri* and *C. angulatus* has been that the large supply of other *Chionoecetes* species on the world market has kept the price too low to offset the high costs of fishing in deep water. Fisheries for other slope-dwelling species, however, have developed when the catches of shallower, related species have declined. For example, in Japan the fishery for *C. japonicus* developed after the local stocks of *C. opilio* declined (Sinoda, 1982). In Alaska, the fishery for the slope-dwelling king crab *Lithodes aequispina* developed after the decline in abundance of the shelf-dwelling king crabs *Paralithodes camtschaticus* and *P. platypus* (Somerton and Otto, 1986). This pattern may be reflected in Alaskan *Chionoecetes* because as *C. bairdi* and *C. opilio* populations in the Bering Sea have declined, landings of *C. tanneri* have increased from a negligible amount in 1992 to 360 metric tons in 1993, and to 414 metric tons in 1994.[1]

Although aspects of the biology of *C. tanneri* have been documented in areas off Oregon (Pereyra, 1966, 1968; Tester and Carey, 1986) and British Columbia (Jamieson et al., 1990), only information on size dis-

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[1] 1995. Alaska Department of Fish and Game, 211 Mission Road, Kodiak, AK 99615. Unpubl. data.

tribution (Hughes, 1981; Alton, 1986) has been reported for Alaskan waters. Furthermore, nothing about the biology of *C. angulatus* has ever been reported. We collected information on both species on a 1982 Japan-U.S. cooperative trawl survey of the continental slope of the eastern Bering Sea. Here we summarize these data, focusing on the depth and size distributions, sizes at maturity, weight-size relationships, and various aspects of the reproductive biology of both species.

Materials and methods

Sampling of *C. tanneri* and *C. angulatus* was conducted from the Japanese stern-trawler, *Ryujin Maru No. 8*, on the continental slope of the eastern Bering Sea between 58.3°N and 60.9°N latitude (Fig. 1). Crabs were captured with a bottom trawl that measured 23 m between the wings, had a codend consisting of three layers of 90-mm mesh, and had a footrope equipped with 55-cm diameter steel bobbins. The study was divided into two parts: from 11 July to 4 August 1982, scientists from the Alaska Fisheries Science Center collected data on all of the biological parameters described below; from 8 August to 25 August, Japanese scientists collected only carapace width data. For both parts, species identification was based on characteristics provided in Garth (1958).

Maximum carapace width of all crabs was measured with vernier calipers to the nearest 1.0 mm, excluding lateral spines. In the first part of the study, both sexes were evaluated for shell condition and females were additionally evaluated for reproductive condition. Shell condition was rated on a 4-point scale, based on hardness, color, and wear of the exoskeleton (see Somerton, 1982), which represents the approximate time interval since the last molt. Briefly, the characteristics of each shell-condition category and its assumed postmolt interval (PMI) are as follows:

1 carapace pliable (PMI <2 wk);
2 carapace hard, little wear on tips of dactyli, few scratches (2 wk <PMI <1 yr);
3 carapace hard, conspicuous wear on tips of dactyli, abundant scratches (1 yr <PMI <2 yr);
4 same as condition 3, except that wear on dactyli is more pronounced (PMI >2 yr).

Reproductive condition was rated on a 5-point scale. Characteristics of each reproductive condition category are as follows:
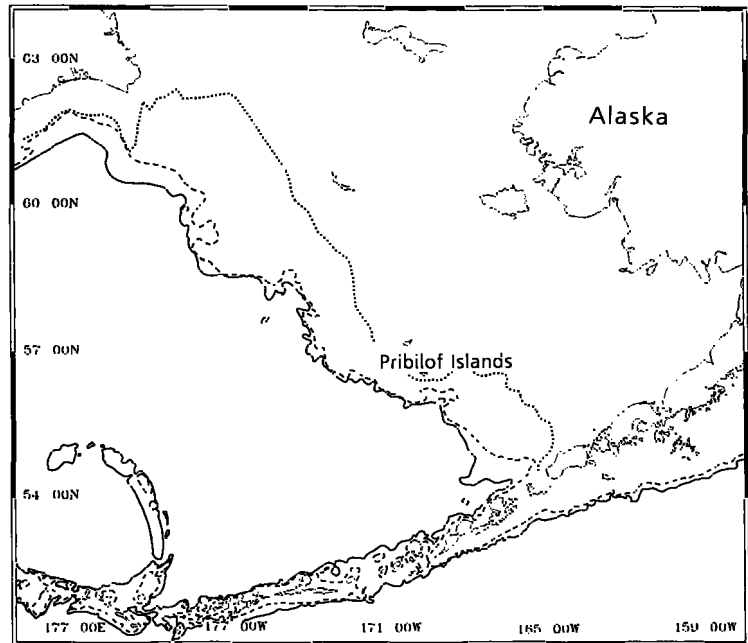

Figure 1

Area surveyed during the Japan-U.S. cooperative survey of the slope of the eastern Bering Sea. The 100-m (dotted line), 200-m (dashed line), and the 1,000-m (solid line) isobaths are shown for the eastern Bering Sea.

1 immature—narrow flattened abdomen;
2 nonovigerous—no embryos or empty egg cases attached to the pleopod setae;
3 uneyed embryos—embryos without conspicuous dark eyes;
4 eyed embryos—embryos with clearly visible dark eyes;
5 empty egg cases—empty egg cases and funiculi attached to the pleopod setae.

Whenever possible, one or more of the following types of data were also collected:

- height of the right chela of males (excluding males with partially regenerated right-hand chela) measured to the nearest 0.1 mm according to the definition in Jamieson et al. (1990);
- total wet body weight of intact males measured to the nearest gram on a triple-beam balance;
- uneyed egg masses from ovigerous females (stored in formalin diluted to 10% with seawater).

Egg masses were processed as follows: mean egg diameter was estimated by randomly selecting 10 eggs from each of 10 randomly selected egg masses and measuring the diameters to the nearest 0.1 mm with an ocular micrometer. Fecundity was estimated

by first air drying the egg masses and, after separating the eggs from the pleopods and setae, weighing them to the nearest 0.1 mg. Two subsamples of about 200 eggs from each dried egg mass were randomly selected, weighed, and counted. Fecundity was then estimated by dividing the total weight of an egg mass by the average of the two estimates of individual egg weight.

Male functional maturity (Conan and Comeau, 1986) was determined from chela allometry. The procedure used is based on the observation that, for *Chionoecetes*, when chela measurements are plotted against carapace measurements on log-log axes, the data conform to two, nearly parallel, straight lines, one representing immature individuals and the other representing individuals that have undergone a puberty molt and have acquired the secondary sexual characteristic of enlarged chelae (Hartnoll, 1978; Somerton, 1980; Conan and Comeau, 1986). We determined with which line an individual observation was associated by using the computer algorithm described in Somerton (1980) to reassign observations iteratively to the two lines until the residual sum of squares was minimized. The carapace width at 50% maturity (W_{50}) for both males and females was estimated by fitting a logistic regression model to the maturity and carapace width data by using generalized linear modeling (Chambers and Hastie, 1992). W_{50} and the variance of W_{50} were then estimated from the parameters of the fitted model with formulas provided in Somerton (1980). In addition to W_{50}, we also calculated the mean carapace width of mature individuals (W_m) as an alternative measure of the size at maturity for comparative purposes.

Weight and carapace width relationships for males of each species were estimated by nonlinear regression (Chambers and Hastie, 1992) to fit a power function to weight and carapace width data. A between-species difference in these relationships was tested by making the relationships linear with a log transformation of the data, and by using analysis of covariance to test whether species-specific relationships fit the data significantly better than a single, combined relationship.
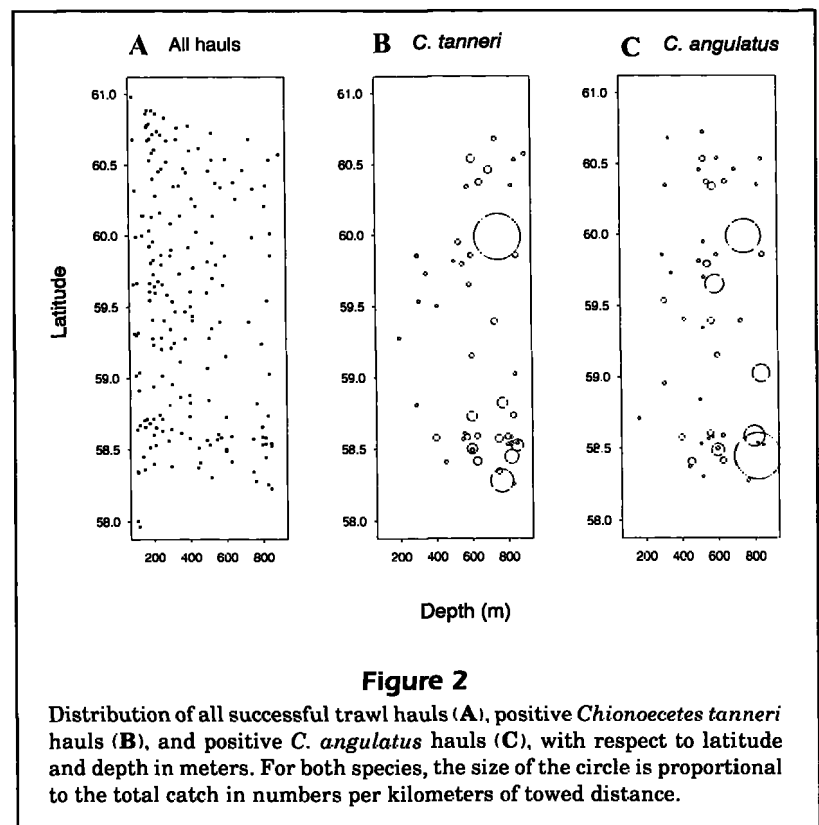
Results and discussion

The 205 trawl hauls that were successfully completed were distributed evenly over the latitudinal range of the survey area (Fig. 2), but fewer hauls were made at greater depths. Over the survey area, both species displayed patchy distributions; much of the catch came from relatively few sampling sites (Fig. 2). *Chionoecetes tanneri* occurred at 47 sites and had a mean CPUE (catch in numbers per kilometer of towed distance) at these sites of 1.9; *Chionoecetes angulatus* occurred at 50 sites and had a mean CPUE of 2.6. The difference in CPUE was not significant (*t*-test, $P=0.418$).

Size distribution

Chionoecetes tanneri males ranged 42–170 mm in carapace width (CW); females ranged 38–126 mm CW (Fig. 3). The maximum size of females was similar to maximum sizes reported off Oregon (126 mm, Pereyra, 1966; 122 mm, Tester and Carey, 1986), whereas the maximum size of males fell between the maximum sizes reported for Oregon (181 mm, Pereyra, 1966; 162 mm, Tester and Carey, 1986). *Chionoecetes angulatus* males ranged 25–160 mm CW; females ranged 35–104 mm CW. The maximum sizes of both sexes were slightly larger than the reported maximum sizes of *C. japonicus* in the Sea of Japan (males 150 mm, females 90 mm, Watanabe and Suzuuchi, 1983).

Figure 2

Distribution of all successful trawl hauls (**A**), positive *Chionoecetes tanneri* hauls (**B**), and positive *C. angulatus* hauls (**C**), with respect to latitude and depth in meters. For both species, the size of the circle is proportional to the total catch in numbers per kilometers of towed distance.
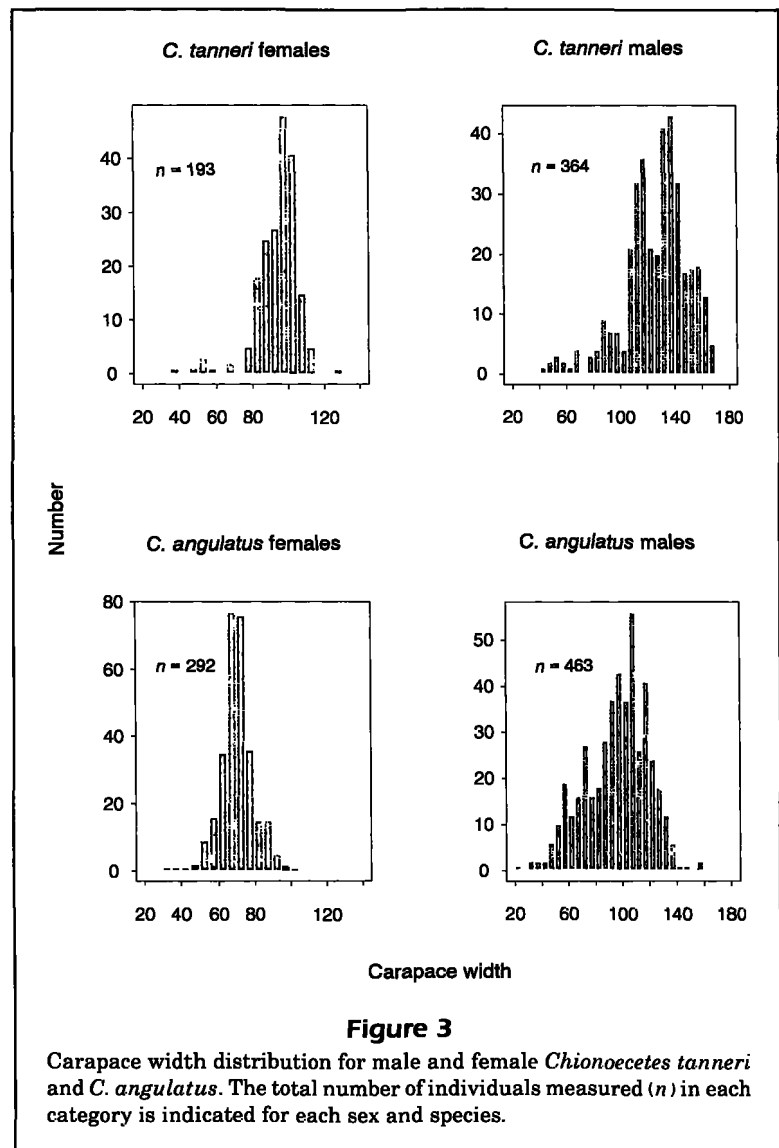
Depth distribution

Both species occurred in the deeper portion of the survey area; few individuals of either species were encountered shallower than 300 m (Fig. 4). For *C. tanneri*, the mean depth of mature males (752 m) was not significantly different from the mean depth of mature females (709 m; t-test, $P=0.38$). This is in contrast to the summertime depth distributions of *C. tanneri* reported off British Columbia (males 580–670 m, females 670–720 m, Jamieson et al., 1990) and off Oregon (males 640–686 m, females 503–549 m, Pereyra, 1966) where mature males were found at distinctly shallower depths than those for mature females. Thus in the eastern Bering Sea, *C. tanneri* does not show a clear depth segregation of males and females as is seen in more southerly latitudes, and the depths occupied by both sexes are greater.
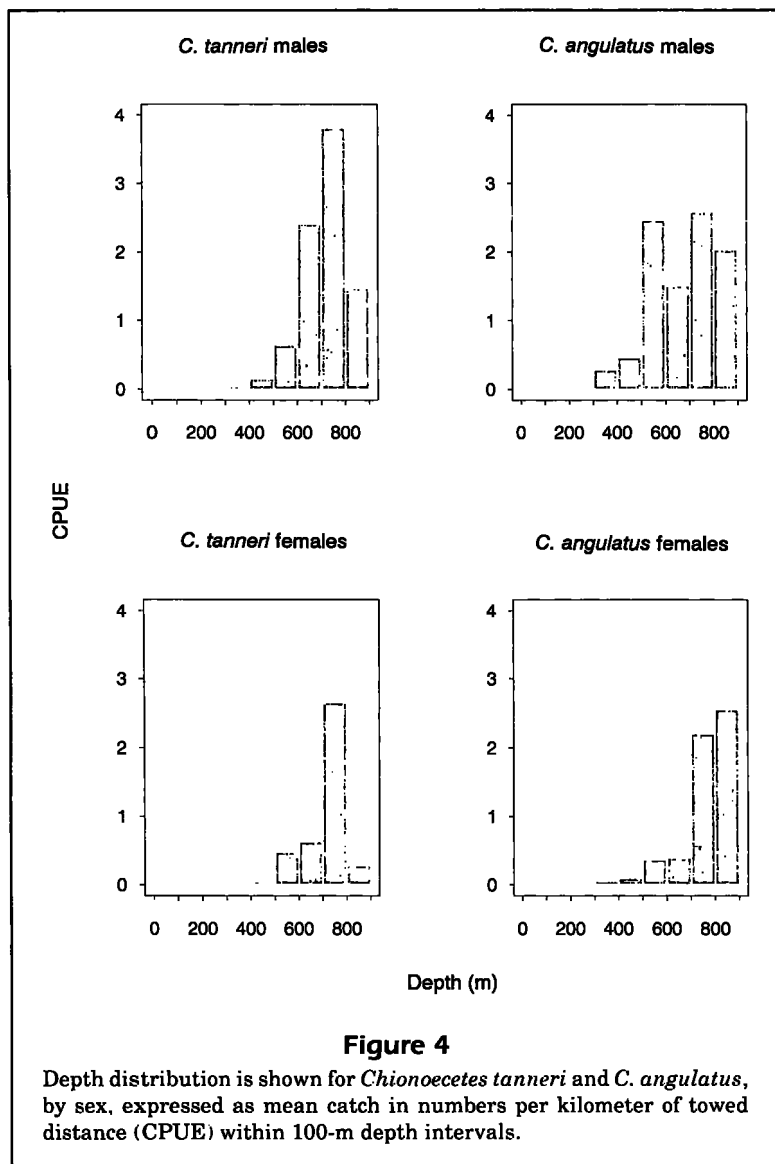
For *C. angulatus*, the mean depth for mature males (647 m) was significantly less than the mean depth for mature females (748 m; t-test, $P<0.001$), indicating that this species does appear to have the same pattern of sexual segregation by depth as that displayed by *C. tanneri* in more southerly latitudes (Pereyra, 1966). The depth distribution reported for *C. japonicus* (Yosho and Hayashi, 1994) indicates that the greatest abundance of both sexes occurs at about 1,000 m. Although this finding suggests that *C. japonicus* may occur deeper than *C. angulatus*, it is clear (Fig. 4) that the distribution of *C. angulatus* extends into deeper water than was covered in our survey and that our estimates of mean depth are low (*C. angulatus* has been reported as deep as 2,974 m [Hart, 1982]; in fact, the type specimen of *C. angulatus* was taken quite near our sampling site in 2,549 m [Rathbun, 1932]).

Juvenile male *C. tanneri* were found in significantly shallower waters than were mature males (t-test, $P<0.001$), whereas juvenile male *C. angulatus* were not significantly different ($P=0.30$) in mean depth from mature males. This is in contrast to the depth distribution reported for *C. tanneri* from British Columbia to Oregon where there is a strong depth segregation by size, where juveniles are found in deeper water than are adults (Pereyra, 1968; Jamieson et al., 1990). The observed between-area difference in vertical distribution indicates that the fac-

Figure 3

Carapace width distribution for male and female *Chionoecetes tanneri* and *C. angulatus*. The total number of individuals measured (*n*) in each category is indicated for each sex and species.

tors producing the size variation with depth at more southerly latitudes do not function similarly in the Bering Sea. Pereyra (1968) hypothesized that *C. tanneri* larvae are advected offshore by Ekman transport and settle to the bottom in deep water. The strong variation in size with depth then results from a shoreward ontogenetic migration of the young crabs. In the region where we surveyed, however, advection of the near-surface water is either quite weak or onshore,[2] rather than strongly offshore. Thus the difference in the observed size variation with depth between the Bering Sea and Oregon may be due to differences in the local oceanographic conditions.

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[2] Pease, C. 1995. Pacific Marine Environmental Laboratory, Seattle, Washington. Personal commun.

Figure 4

Depth distribution is shown for *Chionoecetes tanneri* and *C. angulatus*, by sex, expressed as mean catch in numbers per kilometer of towed distance (CPUE) within 100-m depth intervals.
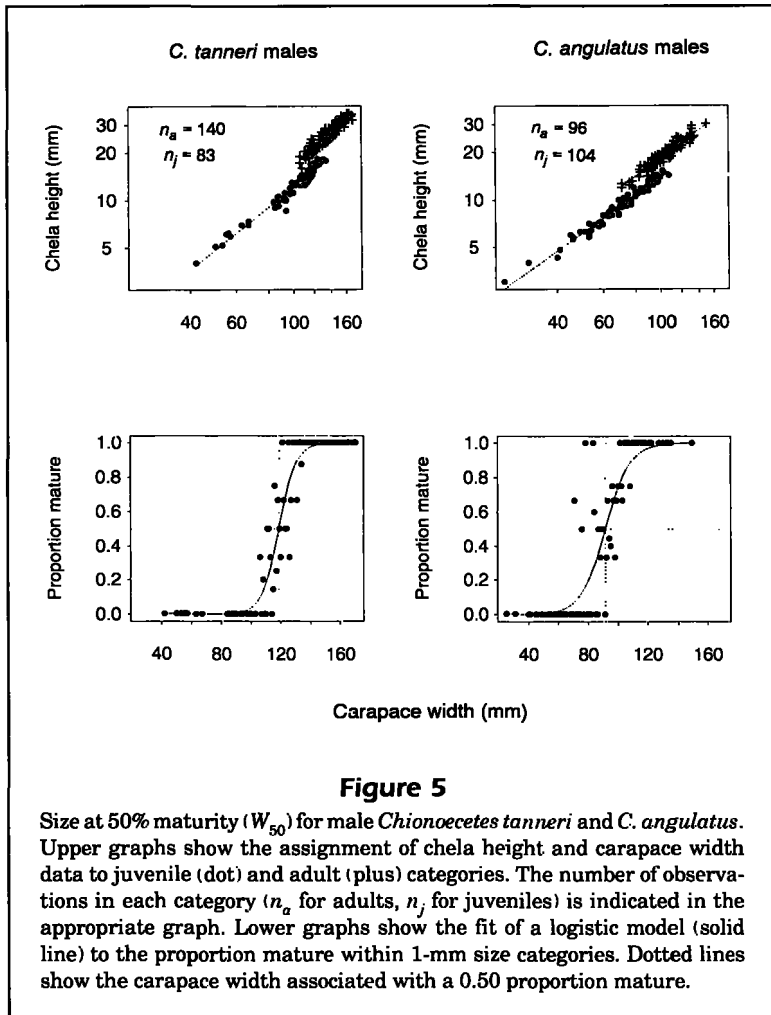
Size at maturity

Estimates of the carapace width at 50% maturity, W_{50}, for both male and female *C. tanneri* (Figs. 5 and 6) were not significantly different from reported values of W_{50} off Oregon (Table 1). Likewise, the estimate of the mean carapace width of mature individuals, W_m, for females was not significantly different from the estimate of W_m for Oregon, but the estimate of male W_m was significantly smaller than the estimate for Oregon (Table 1). Although there may be a slight change in size at maturity from Oregon to the Bering Sea, compared with the large spatial variation in size at maturity observed for the shallow-water species *C. bairdi* and *C. opilio* on the Bering Sea shelf (W_m changes by up to 17% over dis-

tances of 200 km, Somerton, 1981a), the constancy of size at maturity over the latitudinal range of *C. tanneri* is remarkable. Such constancy has been documented before (Tester and Carey, 1986) and has been attributed to the uniformity of water temperature over great distance at the depths inhabited by this species. For *C. angulatus*, the observed estimates of W_{50} (Figs. 5 and 6; Table 1) were similar to values of W_{50} for *C. japonicus* in the Sea of Japan.

Reproduction

Fecundity of *C. tanneri* did not increase significantly with carapace width ($P=0.89$, $n=29$; Fig. 7), primarily because of the large variability in fecundity at size. Over the carapace widths sampled (83–113 mm), mean fecundity was 86,500 eggs. Fecundity of *C. angulatus* displayed much less variability and increased significantly with carapace width (fecundity = $-65,608 + 1,664 \times CW$, $P<0.001$, $R^2=0.55$, $n=24$). For *C. japonicus*, Ito (1976) reported that 70-mm females have about 40,000–50,000 eggs, approximately the same as the fecundity predicted for *C. angulatus* at the same size (Fig. 7). Mean egg diameter was 0.75 mm (SE=0.04) for *C. tanneri* and 0.74 mm (SE=0.04) for *C. angulatus*. Although these estimates are not significantly different from the estimates reported for *C. japonicus* (0.68 mm, Ito, 1976; 0.74 mm, Fukutake, 1965), they are significantly larger than the estimates reported for both of the shallow-water species *C. bairdi* (0.56 mm) and *C. opilio* (0.66 mm, Haynes et al., 1976).

Most mature females of both species carried eggs in the same stage of development (Table 2); therefore it appears that both species have synchronous and seasonal reproduction, in other words, all reproductively active females mate and extrude eggs at about the same time of year. Seasonal reproduction has been previously reported for *C. tanneri* (Pereyra, 1966; Jamieson et al., 1990) and *C. japonicus* (Ito, 1976). However, it has also been reported that *C. japonicus* has a 2-year reproductive cycle (Ito, 1976) and therefore does not have synchronous spawning. If this is true for either *C. tanneri* or *C. angulatus*, one would expect to find more heterogeneity in the observed stages of egg development, unless our macroscopic evaluation of reproductive condition failed to detect differences in embryonic development between the first and second year of a 2-year cycle.

Figure 5

Size at 50% maturity (W_{50}) for male *Chionoecetes tanneri* and *C. angulatus*. Upper graphs show the assignment of chela height and carapace width data to juvenile (dot) and adult (plus) categories. The number of observations in each category (n_a for adults, n_j for juveniles) is indicated in the appropriate graph. Lower graphs show the fit of a logistic model (solid line) to the proportion mature within 1-mm size categories. Dotted lines show the carapace width associated with a 0.50 proportion mature.

Figure 6

Size at 50% maturity (W_{50}) for female *Chionoecetes tanneri* and *C. angulatus*. For each species is shown the fit of a logistic model (solid line) to the proportion mature within 1-mm size categories. Dotted lines show the carapace width associated with a 0.50 proportion mature. Number of adults and juveniles sampled are indicated in each graph.

Synchronous seasonal reproduction is not necessarily the norm for slope-dwelling crabs. For example, the two species of king crabs that also inhabit the eastern Bering sea slope, *Lithodes aequispina* and *L. couesi*, have asynchronous and nonseasonal reproduction (Somerton, 1981b; Somerton and Otto, 1986) as evidenced by a wide variation among adult females in the developmental stages of their embryos. These king crab species also have eggs that are more than twice the diameter of eggs from shallow-water king crabs, such as *Paralithodes camtschaticus*, and have exceptionally large larvae provisioned with a greater amount of yolk (Somerton, 1981b). Such larvae may be lecithotrophic (i.e. nonfeeding) and therefore remain at depth throughout their development. This larval strategy could, in turn, reduce or eliminate larval dependency on the seasonal production of food and thus obviate the need for seasonal reproduction (Somerton, 1981b). For *C. tanneri* and *C. angulatus*, however, the mean egg diameter is only slightly larger than that for the shallow-water species *C. bairdi* and *C. opilio*, indicating that *C. tanneri*
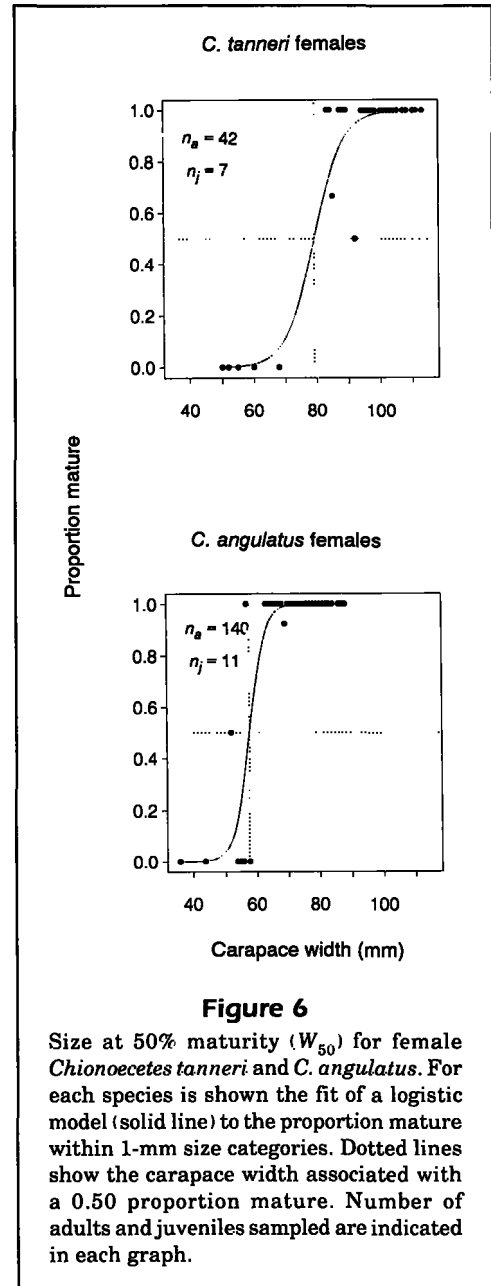
and *C. angulatus* probably have planktotrophic larvae which must migrate to feed in surface waters where prey concentrations are greater. Although such ontogenetic vertical migrations by the larvae of deep-sea fauna were once considered improbable, it is now known that a variety of taxa, from depths even greater than those for *C. tanneri* or *C. angulatus*, possess vertically migratory planktotrophic larvae (Young, 1994).
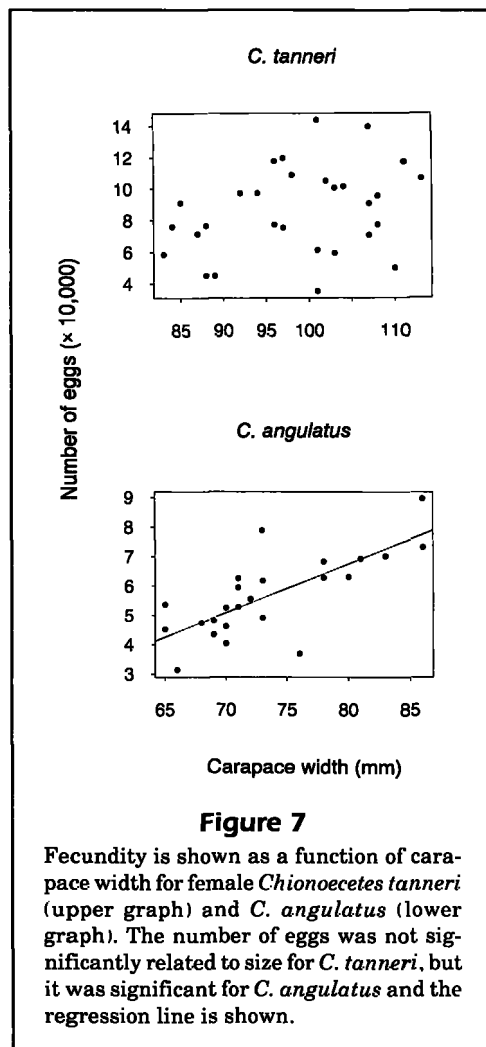
Molting

For mature female *C. tanneri* and *C. angulatus*, relative abundance of the four shell-condition categories

Table 1

Carapace width at 50% maturity (W_{50}) and mean carapace width of mature individuals (W_m), in millimeters, by species, sex, and area. Standard errors are shown in parentheses. Estimates for W_{50} for *C. japonicus* were interpolated from a figure in the noted source and are therefore approximate.

Species	Sex	W_{50}	W_m	Area	Source
C. tanneri	male	118.7 (1.26)	137.9 (1.25)	Bering Sea	This study
	female	79.2 (4.82)	99.5 (1.25)	Bering Sea	This study
	male	118.0	142.7	Oregon	Tester and Carey (1986)
	female	85.0	102.0	Oregon	Tester and Carey (1986)
	male		148.9	Oregon	Pereyra (1966)
	female		102.5	Oregon	Pereyra (1966)
C. angulatus	male	91.4 (1.64)	105.2 (1.58)	Bering Sea	This study
	female	57.8 (1.46)	72.2 (0.52)	Bering Sea	This study
C. japonicus	male	~95		Japan	Watanabe and Suzuuchi (1983)
	female	~55		Japan	Watanabe and Suzuuchi (1983)

Figure 7

Fecundity is shown as a function of carapace width for female *Chionoecetes tanneri* (upper graph) and *C. angulatus* (lower graph). The number of eggs was not significantly related to size for *C. tanneri*, but it was significant for *C. angulatus* and the regression line is shown.

Table 2

Number and percentage of individuals examined in each of three reproductive conditions for mature female *C. tanneri* and *C. angulatus*.

Reproductive condition	*C. tanneri*	*C. angulatus*
3 (uneyed eggs)	33 (79%)	121 (86%)
4 (eyed eggs)	0	2 (1%)
2, 5 (no eggs)	9 (21%)	17 (12%)

did not differ significantly between species (Table 3; $\chi^2=0.27$, $P=0.53$). Most mature females were scored as having shell condition 3 (Table 3), indicating that they probably had not molted for at least 1 year and likely have a terminal molt similar to that of the shallower water species *C. bairdi* and *C. opilio*. Some individuals of both species had molted so recently that their exoskeletons were still pliable. Because the puberty molt is usually associated with mating, some mating must have occurred as late as July. However, the primiparous (shell conditions 1 and 2) females also had a surprisingly high percentage of barrenness (*C. tanneri*—60%; *C. angulatus*—76%) compared with multiparous (shell condition 3) females (*C. tanneri*—16%; *C. angulatus*—3%). For *C. bairdi* and *C. opilio*, primiparous females are rarely barren because mating and egg extrusion quickly follow the puberty molt (Watson, 1970). Perhaps for *C. tanneri* and *C. angulatus*, egg extrusion does not follow a molt as closely as it does for shallower species, and

Table 3

Number and percentage of individuals examined in each shell condition category for adult female and male *C. tanneri* and *C. angulatus*.

Shell condition	C. tanneri	C. angulatus
Females		
1	1 (2%)	4 (3%)
2	4 (10%)	11 (8%)
3	37 (88%)	121 (88%)
4	0	2 (1%)
Males		
1	5 (5%)	20 (21%)
2	123 (88%)	63 (65%)
3	12 (9%)	14 (14%)
4	0	0

Figure 8

Weight-length relationships for *Chiono-ecetes tanneri* and *C. angulatus* and the fitted power curves.

the high incidence of barrenness was due simply to our sampling between times of molting and egg extrusion.

For mature male *C. tanneri* and *C. angulatus*, the relative abundance of the four shell condition categories differed significantly between species (χ^2=21.4, *P*<0.001), primarily because there were considerably more *C. angulatus* males in a recently molted condition (Table 3). The high incidence of recently molted *C. angulatus* males was not due to the chance capture of a large molting aggregation, because recently molted individuals were found at many of the sampling sites. Therefore, it is likely that the timing of the male molting season differs between species.

For both species, however, the relative abundance of the four shell conditions differed between sexes (*C. tanneri*, χ^2=104.1, *P*<0.001; *C. angulatus*, χ^2=130.0, *P*<0.001) primarily because males had lower shell-condition scores than did females. Such between-sex differences in shell condition scores could reflect differences in the timing of the molt relative to sampling, differences in preferred habitat, or differences in adult mortality rate. Alternatively, such differences in shell condition could indicate that mature males have molted more recently, on average, than adult females, raising the question of whether males cease molting at maturity. Jamieson et al. (1990) believed that male *C. tanneri* undergo a terminal puberty molt and are therefore similar to *C. opilio*, for which a male terminal molt has been clearly established (Conan and Comeau, 1986). However, Tester and Carey (1986) also found a between-sex difference, similar to our study, in the index of postmolt age for *C. tanneri* off Oregon; mature males exhibited considerably lower incidence of exoskeleton damage from chitonoclastic bacteria than did mature
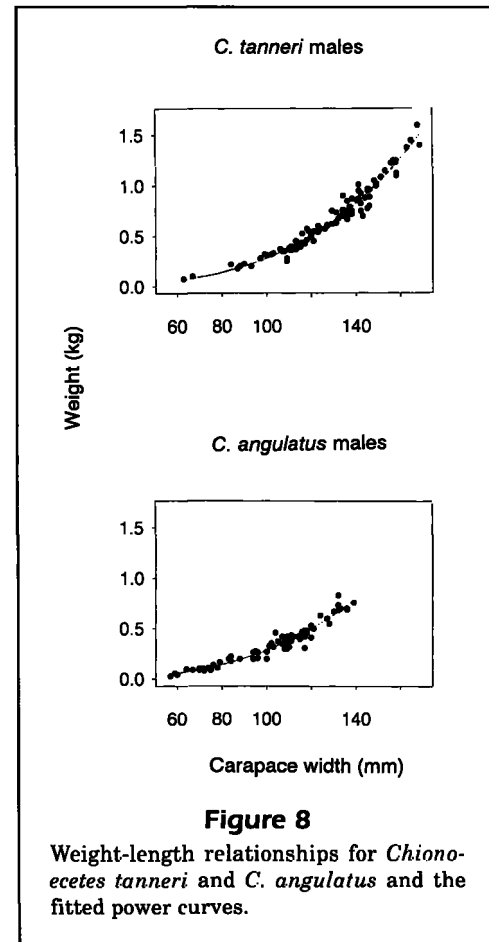
females. This sexual difference in exoskeleton damage was interpreted as an indication that male *C. tanneri* continue to molt after maturity. Although our shell-condition data were consistent with the observations of Tester and Carey (1986), we are not convinced that this indicates that males contintue to molt.

Weight–carapace-width relationship

The increase in male body weight with carapace width (Fig. 8) was not significantly different between the two species (ANCOVA, *P*=0.92; Table 4), therefore a single function was fitted to the combined data. This similarity in the weight-width relationship reflects a remarkable similarity in the shape of *C. tanneri* and *C. angulatus* compared with shallow-water species of *Chionoecetes*. For example, the predicted weight at 120 mm CW is 505 gm for both *C. tanneri* and *C. angulatus* males. The weight of a similar-size *C. japonicus*, another slope-dwelling species, is 588 gm (Watanabe and Suzuuchi, 1983), fairly close to *C. tanneri* and *C. angulatus*. However, the

Table 4

Parameter estimates for the fitted equation weight (gm) = a (carapace width in mm)^b, number of data (n), and goodness of fit (R^2) for male *C. tanneri* and *C. angulatus*, and for both species combined.

	a	b	n	R^2
C. tanneri	1.186×10^{-4}	3.189	101	0.96
C. angulatus	2.244×10^{-4}	3.054	76	0.94
Combined	1.219×10^{-4}	3.183	177	0.97

weight of a similar-size *C. opilio* from the shelf of the eastern Bering Sea is 739 gm (Somerton, 1981c), considerably heavier than the slope species. The likely explanation for this is that slope species of *Chionoecetes*, like slope species of king crabs, have proportionately thinner legs than shelf species (Somerton, 1981b). The evolutionary significance of such depth-related changes in shape is unclear, but for other deep-water crustacea, reduced musculature is assumed to be an adaptation for energy efficiency in a habitat where food is scarce (Childress, 1971).

Similarity of *C. angulatus* and *C. japonicus*

Repeatedly throughout the foregoing discussion, we have compared various distributional or life history characteristics reported from other studies of *C. japonicus* with those determined for *C. angulatus* from our samples because we suspect that the two species actually are either taxonomically identical or that *C. japonicus* is a subspecies of *C. angulatus* (3 years after Rathbun [1932] described *C. japonicus*, Derjugin and Kobjakowa [1935] described *C. angulatus bathyalis* on the basis of specimens that were also collected near Japan). We base our question not only on the similarity of the various biological features that we examined (e.g. size and depth distribution, size at maturity) but also on the high degree of similarity in shape between the two species. We recommend that the validity of the separation of *C. angulatus* and *C. japonicus* be re-examined by qualified systematists.

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