

MOLTING OF FUNCTIONALLY MATURE MALE *CHIONOECETES BAIRDI* RATHBUN (DECAPODA: MAJIDAE) AND CHANGES IN CARAPACE AND CHELA MEASUREMENTS

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ABSTRACT

Laboratory observations with functionally mature male *Chionoecetes bairdi* proved that they can molt. There were 46 males with carapace widths (CW) <119 mm that copulated with primiparous mates in the laboratory and then molted. Two of these males molted twice. After the molt the majority of these 46 males were not as large as males found grasping multiparous mates in nature.

There were 23 males 110–139-mm CW that copulated with multiparous females in the laboratory and were held to see if they would molt. Seventy-four percent of them initiated molting after 26–27 months of captivity. The results of this experiment suggest that molting commonly occurs in males 110–130-mm CW, which are potential recruits to the fishery, and large enough to copulate with multiparous mates. Information on morphometric changes in carapace width and chela height is provided for the molting crabs.

The ability of functionally mature males of the genus *Chionoecetes* to molt, and the relationship of chela size to maturity, are topics about which there has been much recent discussion (Conan and Comeau, 1986; Donaldson and Johnson, 1988). However, the issue of male “morphometric maturity” and its relationship to reproduction became the subject of inquiry after most of the experimental reproductive studies (Adams and Paul, 1983; Paul, 1984; Paul and Adams, 1984; Donaldson and Adams, 1989; Paul and Paul, 1992) had already been carried out for the Tanner crab *Chionoecetes bairdi* Rathbun. None of those studies determined the morphometric maturity status of the males used in the experiments, or their capacity to molt. In this genus, males mature at smaller sizes than females (Paul, 1992), and the amount of sperm delivered to females is not related to male carapace size (Paul, 1984; Sainte-Marie and Lovrich, 1994). However, there appear to be undescribed mechanisms that favor larger males in multiparous matings (Stevens *et al.*, 1993).

The legal size at which male Tanner crabs can be harvested in Alaska is 135 or 140 mm carapace width (CW) depending on the region. Most male Tanner crabs are assumed to be mature at 110–115-mm CW (Donaldson and Donaldson, 1992). These small mature males are protected from harvest with the assumption that they will have

some chance to breed and then grow beyond legal size (Donaldson and Donaldson, 1992). However, Conan and Comeau (1986) reasoned that there was a terminal molt at the onset of maturity in this genus. In this case, some mature males of *C. bairdi* protected by the size limit would never reach legal size. This study provides a preliminary measure of the molting frequency of males >110-mm CW, the potential recruits to the fishery. The experiments were designed to determine if functionally mature male *C. bairdi* could molt, and if so, to identify the changes in chela height (CH) and CW if growth occurred. Males that copulated with primiparous or multiparous mates under controlled conditions were considered functionally mature for these experiments. Males within the same size range as those observed grasping ripe females in nature (Stevens *et al.*, 1993) were used in the observations on molting and growth.

MATERIALS AND METHODS

Males with Multiparous Mates.—Males found grasping multiparous mates in nature are typically >110-mm CW (Stevens *et al.*, 1993). Males of this size were captured with a small otter trawl, fished at 30–60-m depth in Kachemak Bay, lower Cook Inlet, during January 1992. These males were transferred directly to the Seward Marine Center laboratory. There were 23 males with CW 110–139 mm in this group. Multiparous females were captured in the same area using trawls during early winter of 1993. During April and May of 1993, the females were examined daily to see if their eggs had hatched. On the day when all her old egg shells

had been removed, a female was placed in a tank with a single male, where they were observed for copulatory behavior. Throughout this study, copulation was assumed to be successful if the pair adopted the position of male above, female upside down with her abdominal flap open, as illustrated in fig. 3B of Donaldson and Adams (1989). Clutches were examined to see if eggs were fertilized. There were dividing eggs in all the clutches; however, multiparous females frequently had sperm in storage from previous matings (Paul, 1984). Thus, it was not possible to know if the male observed copulating was the parent. After copulation, the tagged male was held until it molted or died. The last observation involving these 23 males was made on 19 April 1994.

In addition to the 23 males above, we included unpublished earlier observations on 4 other males, 130–134-mm CW, that had copulated with multiparous mates and then molted in the laboratory. These males were captured near Homer, Alaska. Their CW and CH measurements are included with those of the 23 males in this experiment to increase the number of morphometric observations.

Male crabs were held communally in running seawater tanks (1 × 4 × 0.5 m deep) with a water exchange rate >100% per h. There were 11 or 12 crabs per tank. The intake for the sea water was at a depth of 80 m, well below the 20-m summer pycnocline, in the fjord. Thus, the laboratory had a temperature and salinity regime suitable for holding crabs. Salinity ranged between 31 and 34 ppt and the sea-water temperature range was 4–9°C during the period when the males captured in January of 1992 were held. All captive crabs were fed twice per week, primarily chopped Pacific herring (*Clupea harengus pallasii* Valenciennes) and other fish species. If a male died while in captivity, it was dissected to see if a new carapace was forming indicating preparation for a molt (Hoenig *et al.*, 1994, their fig. 2C). Observations were ended when all males had either molted or died.

Males with Primiparous Mates.—In the laboratory, we had 46 opportunities to observe growth in CW and CH in male Tanner crabs that copulated with primiparous mates. All the crabs in this experiment with primiparous females were trawled near Homer, Alaska, in 30–60 m of water. These 46 observations were culled from earlier studies (Adams and Paul, 1983; Paul and Adams, 1984; Paul, 1992) designed to examine reproductive biology rather than molting. During those reproductive studies, growth data were recorded, but the experimental design precluded estimating molting frequency for males or their intermolt periods. The thermal and salinity records under which they were held were not available. No comparable molting data were available for immature males.

Maturity status was verified for these 46 males by giving them sole access to a primiparous female ready to ovulate. Females captured as immature individuals were held until their maturity molt. Immature snow crabs are not inseminated before their molt to maturity (Ito, 1963). Immature females were held in communal tanks without males. When one molted, a single male was added to the tank to see if he would copulate. If the eggs subsequently extruded by the female initiated division, the male was considered functionally mature. Then he was tagged with a numbered plastic disk, at-

tached to a leg by a plastic cable tie, and held for varying lengths of time. All 46 of the males used in this report copulated and eggs in the clutches of all their mates initiated division.

Growth Measurements.—For each male, the initial and postmolt CW and CH were measured to the nearest mm. In situ measurements have shown that males grasping primiparous females are much smaller than those courting multiparous mates (Stevens *et al.*, 1993), and our preliminary investigations (unpublished) indicate that some small mature males are unable to copulate with hard-shelled females. Thus, the regressions describing the changes in carapace and chela measurements for males that copulated with primiparous and multiparous mates are treated separately in the figures. The two data sets are also plotted together to show their relative values. Linear regression using the least squares fit and SigmaPlot software was used to plot the relationships between initial and postmolt CW and CH values.

RESULTS

Males with Multiparous Mates

Eleven of the 23 individuals from the 1992 collection that had copulated with multiparous females molted successfully. Five more males started to molt, but died during the process without exiting their old carapace completely, and one started to molt but was cannibalized by his tank mates. Thus, 74% of these functionally mature males initiated molting. The remaining six died for reasons unknown and showed no evidence of a new carapace forming.

The premolt and postmolt measurements of CW and CH for these males is plotted in Fig. 1. The average premolt CW for the molting males was 128 mm (110–139) and CH of 25 mm (18–31). The average premolt CW for the males that died without molting was 136 mm (135–137) and CH of 30 mm (27–35; Fig. 2). Changes in CW and CH during growth of the males that copulated with multiparous mates appear in Figs. 3, 4. Changes in CW for these 15 males were described by the equation: Growth CW (mm) = Initial CW × 1.160 + 0.907; $r^2 = 0.91$, $d.f. = 13$, $P < 0.0001$. The analogous linear model describing changes in CH was: Growth CH (mm) = Initial CH × 0.621 + 19.042; $r^2 = 0.31$, $d.f. = 13$, $P \geq 0.03$. All the males that molted, or died during the process of molting, did so during either March or April 1994 after 26–27 months of captivity.

Males that successfully copulated with multiparous females had CH/CW ratios ranging from 0.16–0.23 (Fig. 5). After cop-

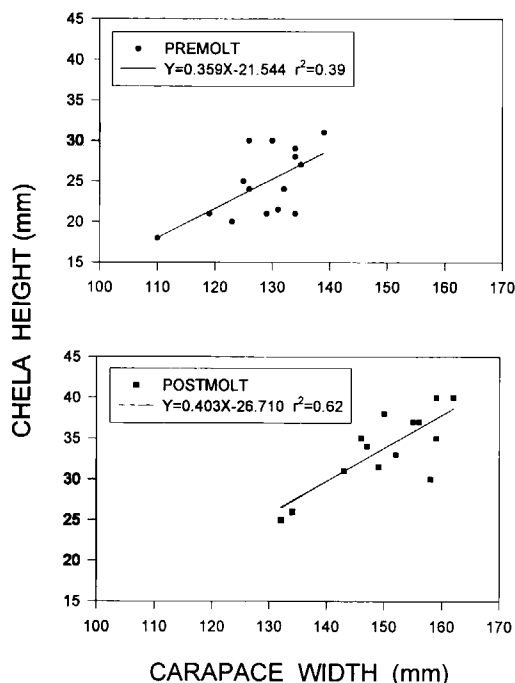


Fig. 1. Measurements of carapace width and chela height in male *Chionoecetes bairdi* that molted after copulation with multiparous mates. Premolt measurements are in the upper panel and postmolt values are in the lower panel.

ulation and subsequent molting, the CH/CW ratio increased to 0.19–0.26 (Fig. 5).

Males with Primiparous Mates

The relationships between CW and CH for these small mature males is plotted in Fig. 6. Increases in CW and CH followed linear models (Figs. 3, 4) for males that copulated with primiparous mates. Growth in CW for the 46 males was described by the equation: Growth CW (mm) = Initial CW \times 1.129 + 5.007; $r^2 = 0.97$, $d.f. = 44$, $P < 0.0001$ (Fig. 3). The corresponding equation describing changes in CH was: Growth CH (mm) = Initial CH \times 1.698 - 4.575; $r^2 = 0.84$, $d.f. = 44$, $P < 0.0001$ (Fig. 4). The change in the ratio of CH/CW for all molting males is shown in Fig. 5. Only 50% of the 46 males that fertilized primiparous mates molted to CH/CW ratio >0.17 (Fig. 5), which is typical of males grasping multiparous females in nature (Stevens *et al.*, 1993).

These 46 males molted during the months of January (4%), February (17%), March

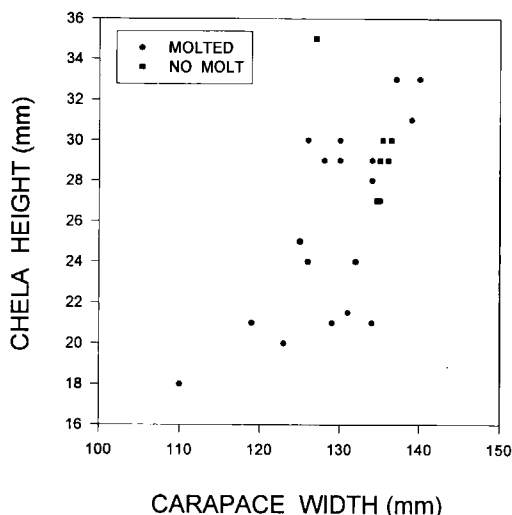


Fig. 2. Measurements of initial carapace width and chela height in male *Chionoecetes bairdi* that molted (circles) or died without molting (boxes) after copulation with multiparous mates.

(66%), and April (13%). Two males that fertilized soft-shelled mates molted twice during the study. One had initial CW and CH values of 86 and 12 mm, respectively, which increased to 105 and 17 mm with the first molt in March 1993, and then to 128 and 28 mm in April 1994. The CW for the other male grew from 82–100 mm, and then to 116 mm. Corresponding changes in CH were 11–14 mm with the first molt, and growth to 21 mm after another 17 months of captivity.

DISCUSSION

In nature, Tanner crabs grasping primiparous mates had an average CW of 106 mm (range 90–120) versus 132 mm (range 100–170) for those with multiparous mates (Stevens *et al.*, 1993). Based on Fig. 3 (upper panel), a crab of 106-mm CW would have to molt at least twice to be as large as the average size male found grasping multiparous mates, 132-mm CW. A 132-mm CW male would grow to 154-mm CW if it molted (Fig. 3 middle panel). Previous observations for Kodiak Island crabs showed that males of 104 mm, and 133-mm CW would grow to 127 and 154 mm, respectively (Donaldson *et al.*, 1981). These results are similar to our own (Fig. 3). The above projections of development assume that male Tanner crabs always exhibit the growth pat-

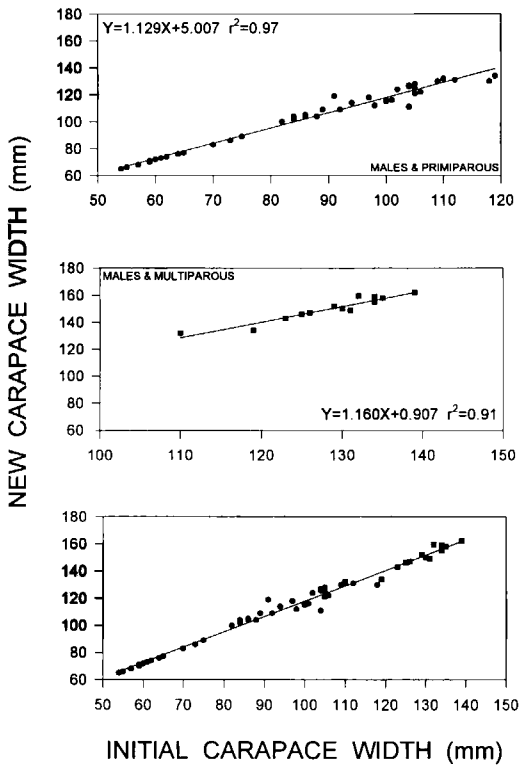


Fig. 3. Change in carapace width in male *Chionoecetes bairdi* that molted after copulation. Males paired with primiparous mates are plotted as circles (upper) and males that copulated with multiparous mates (middle) with boxes. Data for both groups of males are plotted together in the lower panel.

tern shown in Fig. 3. It has been suggested this assumption would be invalidated if the males of Stevens *et al.* (1993) were immature during the preceding instar and had a very large molt increment at maturity. To test this theory, growth measurements on individuals that pass from immaturity to maturity, and on to sizes big enough to fertilize multiparous females, are needed.

Conan and Comeau (1986) concluded that to be mature, male *C. opilio* required "a special molt, which coincides with the differentiation of the claw for grabbing the female." They identified functionally mature males on the basis of carapace and chela morphometry and proposed that this molt to the large claw state was a terminal molt. Males that had reached this large claw terminal molt stage they termed "morphometrically mature." Males that were sexually immature they called "morphometrically immature."

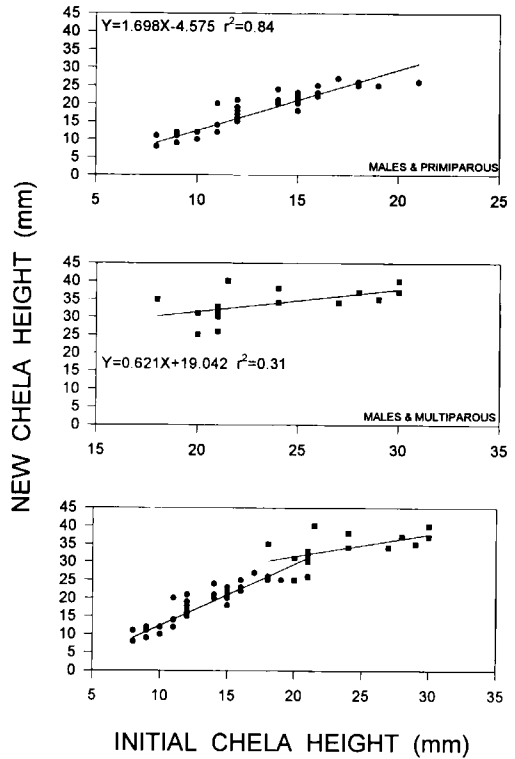


Fig. 4. Change in chela height in male *Chionoecetes bairdi* that molted after copulation. Males paired with primiparous mates are plotted as circles (upper) and males that copulated with multiparous mates with boxes (middle). Data for both groups of males are plotted together in the lower panel.

Our observations on Tanner crabs show that males do not have to be in a terminal instar, or reach their maximum claw size, to be functionally mature. Many of the males that copulated with primiparous females would have been "morphometrically immature" based on the methods of Conan and Comeau (1986). Since they were successful male parents and sexually mature, labeling them "morphometrically immature" creates a contradiction in terms. It now appears that the relationship of "morphometrically mature" or "morphometrically immature" status to sexual maturity is not a simple correlation and the definitions of these two terms from Conan and Comeau (1986) need clarification.

In situ observations noted that most male *C. bairdi* grasping multiparous mates had CH/CW ratios >0.17 and their CH > 17 mm (Stevens *et al.*, 1993). The researchers concluded that a male *C. bairdi* with mea-

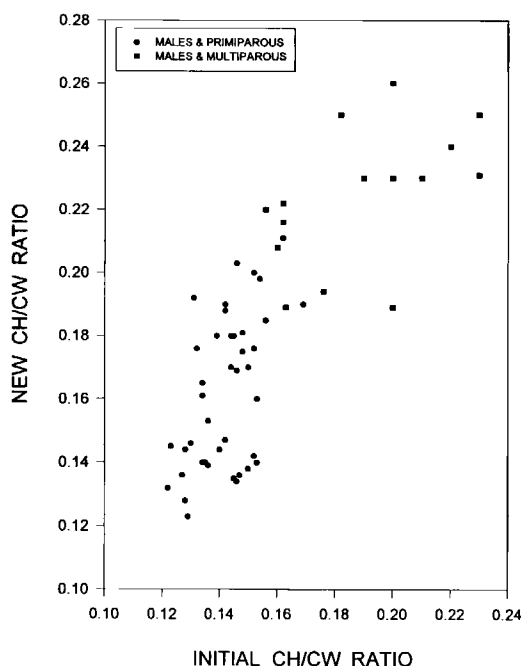


Fig. 5. The initial and postmolt ratios of chela height (CH) to carapace width (CW) in male *Chionoecetes bairdi* that molted after copulation. Males with primiparous mates are plotted as circles and males that copulated with multiparous mates with boxes.

measurements equal to or greater than these values was "morphometrically mature" (Stevens *et al.*, 1993). The authors of that study noted that it was important to know if males with these morphometric characteristics molted. In the laboratory, 76% of the crabs that copulated with multiparous mates and then molted had initial CH/CW ratios >0.17 (Fig. 5) and 100% had CH > 17 mm (Fig. 4). Thus, by the criterion set forth by Stevens *et al.* (1993) which assigns morphometric maturity to males with CH/CW ratios >0.17 , it appears, that "morphometrically mature" males molt. However, it could be argued that using the ratio of CH/CW is not a valid method to assign morphometric maturity; rather the log of CH versus CW should be used. Data on the relationship between CH and CW for males from the study area needs to be gathered prior to making this determination. Currently, only CW measurements are available for males from Cook Inlet.

Donaldson and Johnson (1988) showed molting in male *C. bairdi* from the Kodiak area of Alaska that they categorized as mor-

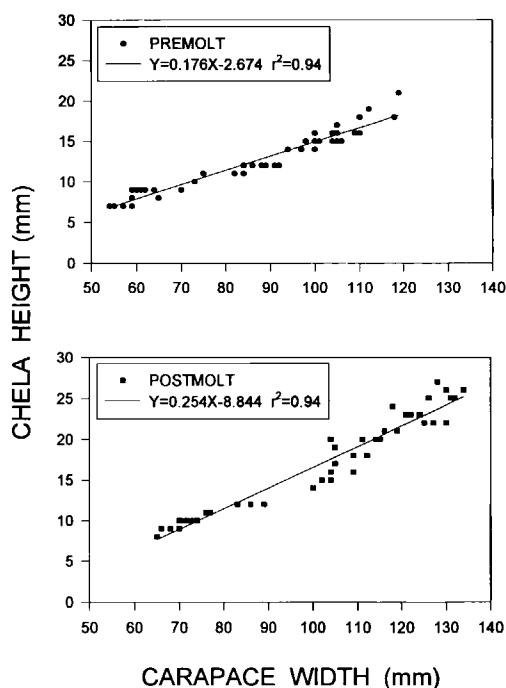


Fig. 6. Measurements of carapace width and chela height in male *Chionoecetes bairdi* that molted after copulation with primiparous mates. Premolt measurements are in the upper panel and postmolt values are in the lower panel.

phometrically mature. However, Conan *et al.* (1988) questioned the validity of their classification of molting males as being morphometrically mature. This controversy seems to arise from the fact that the alteration in male CH with maturity is not an obvious change, like that seen with the female abdominal flap. Therefore, correct assignment of every individual to the correct status is problematic (Conan *et al.*, 1988).

All males that molted in this study did so between January and April. These months are also the breeding period for this species (Adams and Paul, 1983; Paul *et al.*, 1995). Recent studies have demonstrated that Tanner crab males do not breed for at least 90 days after molting, even when isolated with receptive females (Paul *et al.*, 1995). Newly molted males have a soft carapace, and reduced musculature and gonads. Males that molt before the breeding season may forgo breeding that year. Alternatively, some males may breed and then molt. It is presumed that males 110–115-mm CW will have a chance to breed before being sus-

ceptible to commercial fishing (Donaldson and Donaldson, 1992). However, since a male's chance to breed is constrained not only by his size, but also the timing of his molt, molting chronology should be considered when estimations of male parent populations are made.

Males big enough to copulate with multiparous mates had to be held for over two years before they molted. None of them were soft-shelled at capture; therefore, their intermolt period was longer than the time we can account for. It is possible that laboratory conditions either retarded or hastened the molting process, but in situ observations also suggest that males > 110-mm CW have long intermolt periods. In one study, 47% of tagged male *C. bairdi* > 110-mm CW were recaptured after two years and another 7% after three years (Donaldson, 1980). Thus, it appears that male Tanner crabs in the Gulf of Alaska, > 110-mm CW, have intermolt periods exceeding two or more years. In the colder environment of the Bering Sea, intermolt periods may be markedly longer than those Tanner crabs in the Gulf of Alaska. In situ tagging observations, and laboratory growth studies, designed to measure intermolt periods relative to temperature, would improve estimates of recruitment to the fishery. Study designs dealing with molting in mature male *Chionoecetes* spp. should take into consideration the possibility that the intermolt periods may span several years.

The controversy over terminal molt in male *Chionoecetes* spp. and the "morphometric maturity" status of the male parents (reviewed in Dawe *et al.*, 1991) posed the question: do functionally mature males molt? A previous growth study (Donaldson *et al.*, 1981) showed molting in male Tanner crabs large enough to be mature (> 110-mm CW) and this study verified that males proven to be functionally mature can molt. Fishery managers have assumed that male Tanner crabs mature at 110–115-mm CW and that most of them will recruit to the fishery (Donaldson and Donaldson, 1992). In this study, 74% of the prerecruit size males held to determine molting frequency molted. This observation supports the premise (Donaldson and Donaldson, 1992) that molting is common for mature prerecruit male Tanner crabs in the Gulf of Alaska. If Tanner crabs in the Gulf of Alaska have a

terminal molt, this study suggests that for many males it occurs after they exceed the legal size. However, 26% of the males that copulated with multiparous mates died without molting. These males tended to be some of the largest individuals in the experiments (Fig. 2) and could have been at the end of their natural lives. The non-molting males may have reached their genetically controlled maximum size and never had the potential to recruit to the fishery. Alternatively, they may have died prematurely in captivity. Additional observations need to be completed to identify which of the above alternatives is correct. In situ studies, using internal tags, radiometric measures, or other methods, should be conducted to identify geographic variations in male molting frequency and to estimate the length of their intermolt period.

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