Observations From a Submersible Shed New Light on Crab Behavior

Any scientist who has conducted trawl surveys has firsthand knowledge that most organisms are not randomly distributed throughout their environments. This is especially true for crabs. Many tows produce few or no crabs at all, while some will plug the net with a "beetle-bomb"—thousands of crabs, typically of the same sex and size. Observations made near Kodiak, Alaska, using the submersible *Delta* (Fig. 1) in 1991-92 have provided us with new insights into the behavior causing aggregations of Tanner crabs (*Chionoecetes bairdi*).

From January through March, male and female crabs migrate into shallow (2-15 m) water to mate. There, male crabs grasp females in a mating embrace (Fig. 2) which may last up to 2 weeks. Prior to mating, the female (termed pubescent at this time) must undergo a maturity molt. The male protects her from predators and competing males, while the female sheds her old shell. Several hours after the female has molted, the male and female mate, after which the crabs separate. The female extrudes a clutch of bright orange eggs, usually within 24 hours after mating, and is then termed primiparous. Some males mate with multiple females (up to 10 in laboratory aquaria), but females probably do not mate again in the same season. After mating for the first time, female crabs migrate to deeper water. Females do not molt again after reaching maturity. Multiparous crabs, which must remate in a hard-shell condition, are rarely observed in shallow water.

In 1991, I began to investigate the size relationships of mating Tanner crabs along with Jan Haaga and Eric Munk (National Marine Fisheries Service, Kodiak Laboratory) and Bill Donaldson (Alaska Department of Fish and Game). During 1991-92, we collected more than 120 pairs of crabs by scuba in shallow water (< 15 m). Virtually all were pubescent females paired with small (=107 mm width) males; the males, however, had relatively large chela (Fig. 3) and therefore were considered morphometrically mature. In order to determine what size males mated with multiparous females, it was necessary to capture grasping pairs from deep water. Using the submersible *Delta* was considered to be the only method for doing this.

The *Delta* is a two-person, one-atmosphere sub, with a working depth of 400 m. It is equipped with a two-fingered mechanical arm which we modified by adding six extra fingers (the "grabber"). Crabs captured with the arm were placed into a plastic sampling basket from which they could not escape. An external video camera viewed and recorded a path slightly over a meter wide.

In late April 1991, we began searching Chiniak Bay with the *Delta* at depths of 100-150 m for the presence of grasping crabs. Crabs were distributed sparsely (0.05 crab/m^2) over most of the bottom. After 4 days, we discovered a dense aggregation unlike any we had ever seen. Our first glimpses were of low mats of female crabs (Fig. 4) piled two or

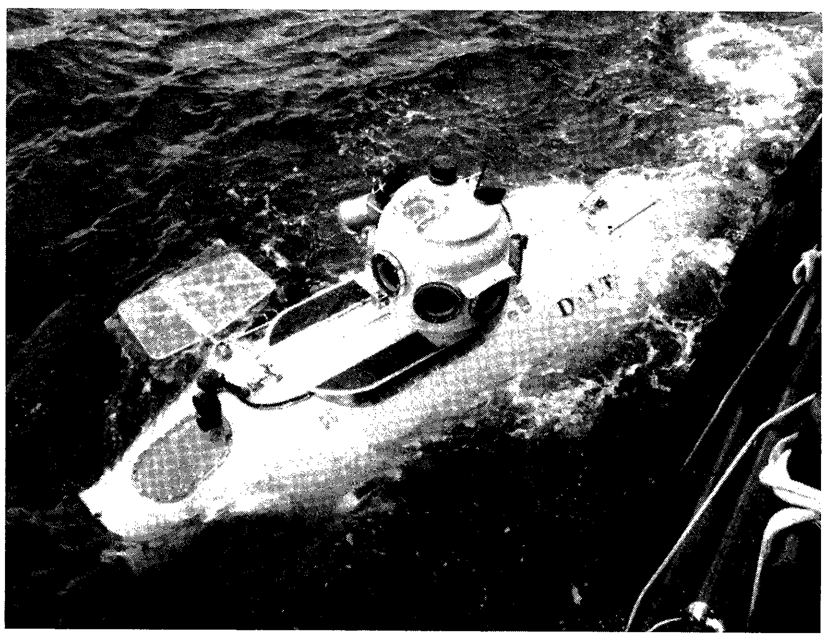

Figure 1. The two-person submersible Delta can dive to 400 m and collect a variety of information. The basket used for holding captured samples is on the starboard side of the vessel beneath the Plexiglas diving plane.

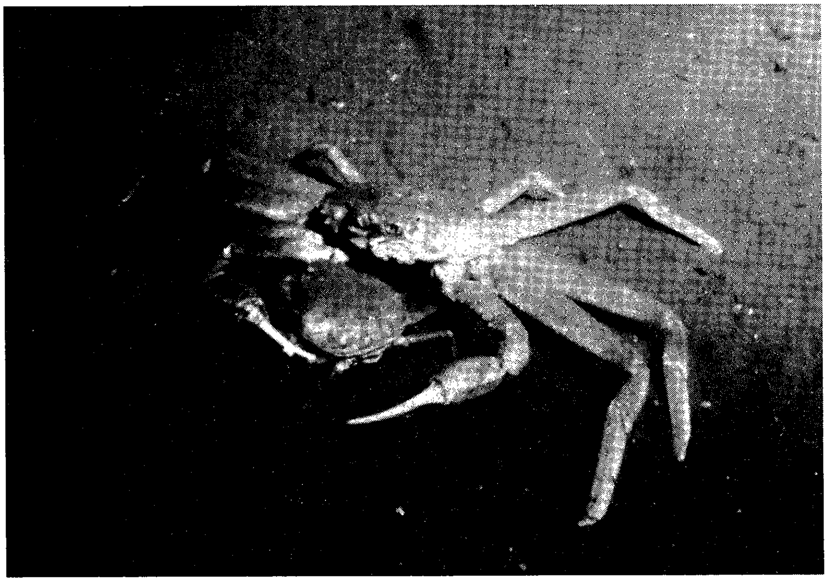

Figure 2. A mature male Tanner crab grasps a smaller female in a premating embrace.

three deep over several square meters of bottom. After several more days of diving, we realized that such piles were only a small portion of a much larger aggregation covering an area approximately 150 m x 150 m (about 2.2 ha). In the center of the aggregation, females formed dome-shaped mounds (Fig. 5) about 1 m in diameter and 0.5-1.0 m high. The mounds were regularly spaced on the seafloor at intervals of 2-3 m and contained 100-400 crabs each. All crabs in the mounds appeared to be multiparous females with eyed eggs about to hatch. While examining the aggregation and searching for paired crabs, we literally plowed into mounds, stopping the *Delta* and scattering crabs over and around the vessel. Often, we turned away from one mound and immediately crashed into another, like a pinball bouncing off the bumpers. On one dive transect of 50-m length, 19 different mounds were encountered.

Males were present in low numbers (1-10 per 100 females) and were distributed mostly around the outside of the aggregation, where they were mating with individual females. Using the grabber, we were able to capture 47 pairs from the aggregation. Males mating with multiparous females were larger (=120 mm) than those we had observed mating with pubescent females in shallow water. Although male crabs as small as 60 mm will mate with females in laboratory aquaria, our data show that only those crabs with large claws participated in mating in the ocean, the few exceptions mostly having regenerated claws. Crab counts obtained from the video recordings were averaged over 10-m intervals and mapped (Fig. 6), showing the size of the aggregation. Crab densities in the aggregation were 2-3 orders of magnitude greater than densities in the surrounding area. Summation of crab densities over the mapped area (0.25 km^2) provided an estimate of 100,000 crabs.

In early May 1992, we revisited the same site with the *Delta*, with the goal of capturing females, counting piles, and determining the number of crabs present. Unfortunately, we discovered during our first dives that nearly all the crabs had mated and dispersed,

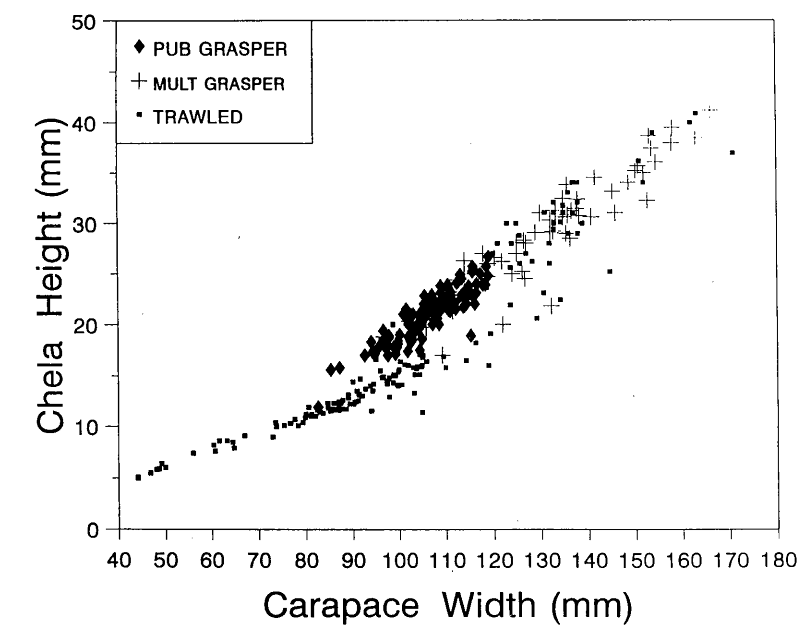

Figure 3. Relationship of chela height to carapace width for male Tanner crabs by pairing status. Pub grasper = male grasping pubescent female (collected by scuba). Mult grasper = male grasping multiparous female (collected by submersible). Pairing status of trawled crabs is unknown.

probably due to warmer (5.4°C vs. 3.6°C) water. The highest crab density observed was only 2.2/m^2 (vs. 100/m^2 in 1991). Over 85% of the females were buried in the mud, and of those, 88% had extruded new clutches. But some females remained active on the surface, and 75% of those had not remated. This activity pattern reversed at night, when 71% of females were surface-active. Thus, after mating, females resumed a diel rhythm of nocturnal foraging alternating with diurnal burial. In 1992, crabs were spread out over a much larger area (25 ha) at lower densities (0.3/m^2) than in 1991, but a similar number (75,000) were present. The large number present in 1991 was probably drawn from a relatively small local area. We also observed dead mature crabs of both sexes in the area of highest density, suggesting that some mortality occurred after mating, perhaps as a result of the combined effects of exhaustion, starvation, and senescence.

These observations have led to a complete reexamination of our existing paradigm of mating in *Chionoecetes* and other genera of the family Majidae. (In a serendipitous event, we also discovered nearby two similar aggregations of the closely related lyre crab, *Hyas lyratus*. Although we had long suspected that crabs were semi-gregarious, especially when mating, we had no idea of the intensity or scale of such aggregations. An extensive literature search turned up anecdotal observations of aggregative behavior in seven other species of Majid crabs, suggesting that rather than being unusual, such behavior may be characteristic of the family. Our observations are the first directed study of such behavior.

The results of our investigations have led to many more questions about the aggregative behavior of crabs. What is the purpose of aggregation? Does mound-forming concentrate an odor trail which attracts males, thereby increasing mating opportunities? Do females form mounds to delay mating or to prevent multiple matings? Does mound-forming provide the larvae access to better

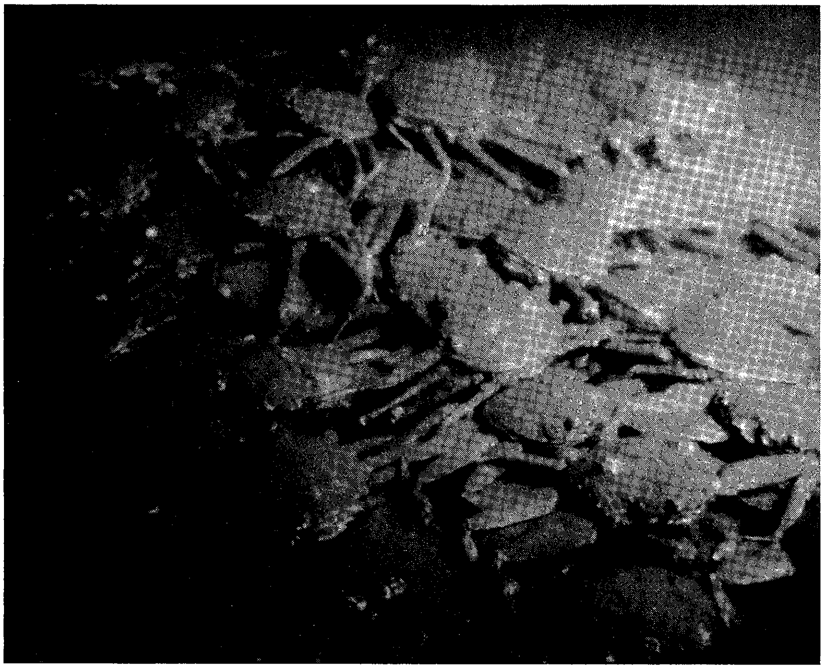

Figure 4. Early stage of mound formation consists of a mat of female crabs in one to two layers.

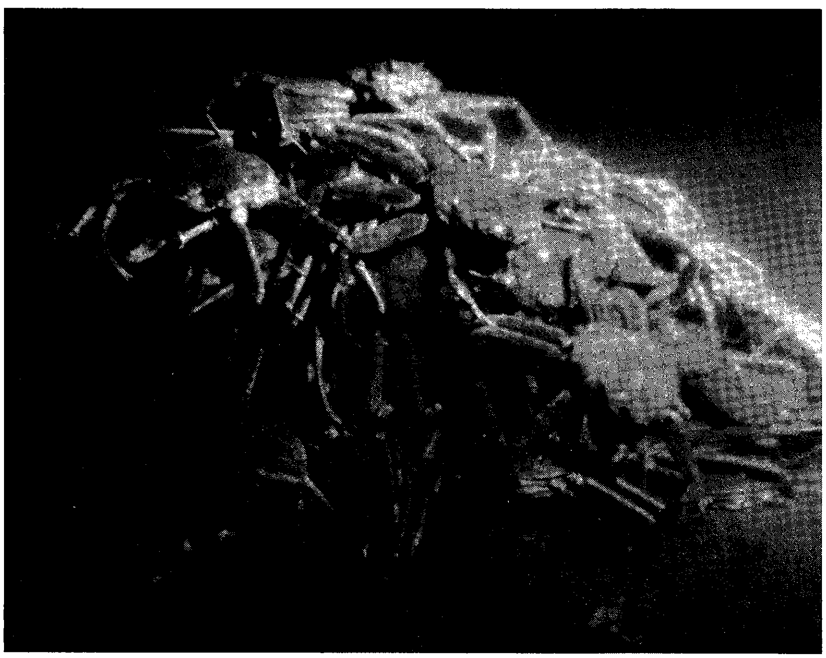

Figure 5. Typical pyramidal mound of female Tanner crabs with cloud of suspended sediment particles trailing off to right. Note that barnacles indicate advanced shell age.