INFORMATIONAL LEAFLET NO. 256

AN ETHOGRAM AND DESCRIPTION OF MATING BEHAVIOR
FOR THE TANNER CRAB, Chionoecetes bairdi M.J. RATHBUN

By
William E. Donaldson
and
Albert E. Adams

STATE OF ALASKA
Bill Sheffield, Governor
DEPARTMENT OF FISH AND GAME
Don W. Collinsworth, Commissioner
P.O. Box 3-2000, Juneau 99802

June 1986

AN ETHOGRAM AND DESCRIPTION OF MATING BEHAVIOR FOR THE TANNER CRAB, *Chionoecetes bairdi* M.J. RATHBUN

By

William E. Donaldson

and

Albert E. Adams[1]

Alaska Department of Fish and Game
Division of Commercial Fisheries
Kodiak, Alaska 99615

June 1986

[1] University of Alaska, Fairbanks

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Laboratory observations of mating and the constituent behavioral actions of the Tanner crab, *Chionoecetes bairdi*, are herein defined, described, and compared with similar phenomena in other brachyuran crabs. Twenty-seven distinct actions were observed as performed by *C. bairdi* during 133 matings. Seven actions, carapace caressing, bouncing, body lifting, palpitating, sternum-to-sternum positioning, intromission, and pull-up were unique to reproduction. Only five actions (grasping, antennule flicking, sternum-to-sternum positioning, vigorous moving of mouth parts and intromission) were common to every completed copulation. Most primiparous females mated shortly after their maturity molt while in a new, soft-shell condition. However, other primiparous females mated in a semi-hard-shell condition as late as 21 days after the maturity molt and still produced viable zygotes. Multiparous females were able to fertilize eggs with sperm stored in their spermathecae during the preceding breeding season. Breeding recurred when males were present at the time multiparous females were receptive (during and shortly after the hatching of their eggs). Courtship, which is subtly developed, entails precopulatory attendance of the female by the male and performance of actions (body lifting, beating, and kicking) which quiet the female if she attempts to escape. Ungentle male-female interactions were infrequent when the female's exoskeletal condition was new and soft, more frequent when the female had a new semi-rigid exoskeleton, and prevalent when the female had an old, hard exoskeleton. In consequence, both the ability of the females to thwart breeding attempts by small and/or weak males and the occurrence of grasping marks on female exoskeletons directly increased with exoskeletal hardness. Instances are noted in which more than one male copulated with individual females.

KEY WORDS: Tanner crab, *Chionoecetes bairdi*, mating behavior, molting.

INTRODUCTION

The brachyuran crab, *Chionoecetes bairdi* Rathbun, is widely distributed in the northern North Pacific Ocean between the central Bering Sea and the State of Oregon (Garth 1958; Hosie 1974) and has supported major fisheries from Japan, the Soviet Union, and the United States (Brown and Powell 1972). Consistent declines in commercial catches since 1978 (Colgate 1982) have prompted investigations of biological and environmental factors which are affecting population sizes and distribution of *C. bairdi*.

Reproductive behavior and potential in the genus *Chionoecetes* have been the topics of several studies. Investigators have described and/or measured fecundity (Brunel 1962; Ito 1963, Watson 1969; Kon 1974; Hilsinger 1975 and 1976; Haynes et al. 1976; Thompson 1979; Paul 1982; Adams and Paul 1983), size at maturity in males (Bright 1967; Kon et al. 1968, Sinoda 1968; Ito 1970; Watson 1970; Brown and Powell 1972; Kanno 1972; Hilsinger et al. 1975; Kon 1980; Somerton 1980 and 1981), and generalized mating behavior (Watson 1970 and 1972; Takeshita and Matsuura 1980; Adams 1982). The purpose of our paper is to provide a descriptive catalog of action patterns (an ethogram) for *C. bairdi* behavior with emphasis on mating. As far as possible, we utilized terminology established by previous authors.

The reproductive behavior of *C. bairdi* can be better understood with background knowledge of major events in the animal's development and life history. Therefore, a concise overview is presented for those readers who are not familiar with this decapod. Sexual dimorphism is first apparent during early instar (juvenile) stages. Differential growth patterns further accentuate the dimorphism between females and males (Donaldson et al. 1981). The latter grow through most of their lives, although the occurrence of males with very old shells indicates the entire adult male population does not grow annually. In contrast, females attain their maximum size during a final molt to maturity which takes place from late December to early June.

Females are sexually receptive immediately after their maturity molt and remain so for at least another 21 days. Minutes after molting, primiparous[1] females are flaccid, incapable of evasion, and vulnerable to mating with males even 25 or 30 mm smaller (carapace width). Exoskeletal rigidity rapidly increases, within hours after the molt, thus enabling females to escape from smaller males (Adams 1982). Mated primiparous females carry their attached, developing eggs until May or early June of the succeeding year (approximately 15 to 17 months) at which time hatching occurs. Our laboratory observations reveal that these individuals may then either remate or utilize sperm stored in their paired spermathecae from the previous year's mating to fertilize the next egg mass. As a multiparous spawners, the female carries the developing eggs for approximately 12 months (until May or June) at which time they hatch and she may

---

[1] An adult female crab is termed primiparous depending upon whether it is about to produce, is producing, or has only produced its first egg mass or multiparous, has produced a subsequent egg mass.

again mate or produce a viable clutch utilizing stored sperm. The temporal difference between incubation periods of primiparous and multiparous egg masses has not been explained, nor do we know the total period over which this species retains its ability to reproduce[1].

METHODS

Live *C. bairdi* were captured in otter trawl tows and by SCUBA at Woman's Bay and Chiniak Bay near Kodiak, Alaska by Alaska Department of Fish and Game (ADF&G) biologists during the winters of 1979-1982. The crabs were then transported to Seward, Alaska where they were held and observed at the Marine Science Center (operated and maintained by the Institute of Marine Science, University of Alaska, Fairbanks). Holding facilities consisted of seven cylindrical plastic tanks-four with capacities of 1,895 liters and three at 1,620 liters. Natural sea water was continuously pumped into the laboratory tanks from a depth of 60 meters in Resurrection Bay. During the observation period, temperatures normally remained between 4 and 6°C, and salinity between 30 and 34$^{0}/_{00}$. A 168 liter aquarium was used to most observations, while 10 matings were observed in a 120-liter wooden tank with gravel substrate. Additionally, Tanner crabs were held for observation in a 465 liter aquarium at the ADF&G facilities in Kodiak, and observations were made to verify the observations from the Seward facility.

Most observations were made at night to minimize external distractions. Overhead lights were turned off and a low intensity side light was used to permit observations. Observer movements were minimized and behavior documented in written notes, on audio magnetic tape and with photographs. Tanks were emptied and cleaned after each mating.

To distinguish size-related behavioral phenomena we assigned males to the following three size categories (based on carapace widths: small (50 to 79 mm); equivalent in size to females (80 to 119 mm); and large (120 mm or greater). Carapace width was measured across the widest part of the branchial region of the carapace with a steel vernier caliper.

RESULTS

Tanner crabs displayed a diverse array of body movements in performing the basic life functions of respiration, feeding, waste elimination, locomotion, and mating. Some movements, such as grasping, were common to different types of behavior (Table 1). Others were unique to a particular behavior pattern or were sex-specific. During the three-year study period, 118 primiparous and 15 multiparous *C. bairdi* matings were observed. Reproduction entailed the

---

[1] Based on cohort analysis, Somerton estimates the maximum reproductive potential of female Tanner crab in the Eastern Bering Sea does not exceed 5 years. (Somerton 1981, p. 77)

Table 1. Behavioral context of actions performed by female (F) and male (M) Tanner crab, *Chionoecetes bairdi*.

Behavior type / Action:	Feeding	Body waste elimination	Locomotion/ Exploration	Agonistic Interactions w/intra-specific rivals	Mating	Brood care
High-on-Legs	M		F, M	F, M	M	F
Grasping	F, M		F, M	F, M	F, M	
Antennule flicking	F, M	F, M	F, M	F, M	F, M	F
Pushing				F, M	F, M	
Submissive posture				F, M	F, M	
Stroking	F, M		F, M		M	
Rubbing	F, M		F, M		M	
Poking					M	
Body Lifting					M	
Bouncing					M	
Beating				M	M	
Kicking				F, M	F, M	
Carapace caressing					M	
Assisting in molt					M	
Leg encircling	F, M			F, M	M	
Leg interposing	F, M			M	M	
Vigorous movement of mouth parts	F, M	F, M			F, M	F
Abdomen flapping		F, M			F, M	F
Palpitating					M	
Sternum to sternum position					M	
Intromission					F, M	
Pull-up						F

-Continued-

Table 1. Behavioral context of actions performed by female (F) and males (M) Tanner crab, *Chionoecetes bairdi* (continued).

Behavior type: / Action:	Feeding	Body waste elimination	Locomotion/ Exploration	Agonistic interactions w/intra-specific rivals	Mating	Brood care
Maxilliped tap					M	
Pleopod combing					F	F
Clasping and pulling at pleopods					F, M	F
Pleopod waving and flexing					F, M	F
Stretching					M	

greatest number of unique actions. These are described below along with movements which, although not exclusive to reproduction, regularly occurred during mating. A sequential series of photographs (Figures 1-10) shows various stages of the molting and mating acts. These figures are further referenced in the text when the behavior discussed was captured in the photograph.

Grasping (Figures 1, 2, 4-8)

A crab extends one or both chelipeds (with tips widely opened) toward another crab or object and, upon contact, secures a hold by gripping it. Duration of the grasp varied greatly from a few seconds to 151 hours[1]. The longest times were recorded when large males grasped with either females which were days away from their maturity molt or multiparous females whose eggs were in the process of hatching (Adams 1982).

Grasping could be initiated quite unexpectedly because no consistent approach existed and individuals moved at different speeds. Usually the grasper actively searched for the graspee. Sometimes the grasper was initially physically contacted (stepped on or brushed against) by the graspee. Less frequently the grasper seemed to make contact accidentally after moving close to (or even bypassing) the graspee. Motion speeds varied from slow approaches and pursuits to sudden lunges or rapid chases. Prior events affected the relative positions of the grasper and graspee at the initiation of grasping. However, in every completed copulation the male eventually held the female in such a way that she faced him rostrum-to-rostrum. Often the male manipulated the female into this position after initially grasping her from behind or from one side.

Recently molted females (juveniles and adults) were grasped with surprising gentleneness such that their soft, new cuticle was only slightly indented by the male's chela(e) and no discernible marks resulted. Most hard, old-shell multiparous females were subjected to more forceful grasps by males as evidenced by the deep, pinkish-white scratches and punctures on their pereiopods[2]. In extreme cases, multiparous females lost one or more pereiopods as a consequence of the force exerted by the attending male.

Grasping was not restricted to reproductive behavior. *C. bairdi* of all sizes and both sexes temporarily grasped: (1) food; (2) other crabs which were consuming food; (3) potential competitors for the same and other species; and (4) objects which they encountered during normal locomotion and exploration. In these instances the nonreproductive objective of the grasper became obvious when no further actions were taken toward mating.

---

[1] For *C. opilio*, this precopulatory embrace may last up to eight days (192 hrs) (Watson 1972).

[2] In a sample of adult female *C. bairdi* from the Eastern Bering Sea, 83.5% had discernible grasping marks (Somerton 1981).

PLATE I

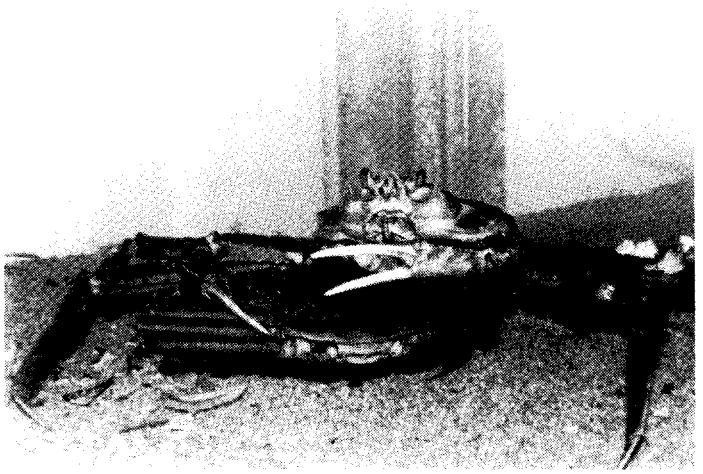

Figure 1. Male C. bairdi grasps female with his right chela in preparation for her molt to maturity.

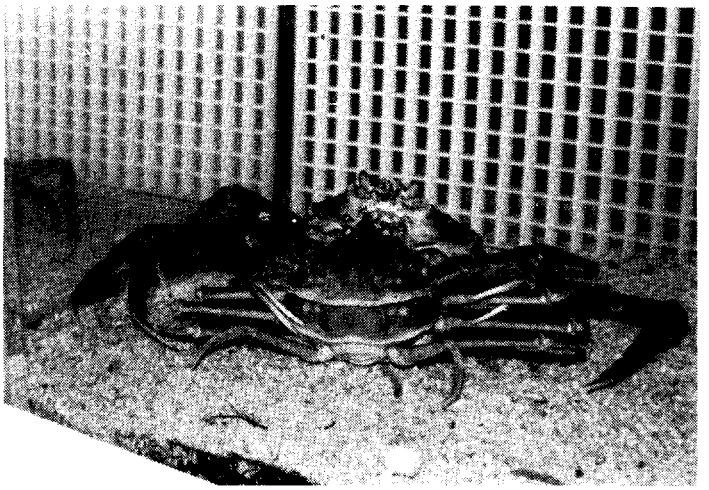

Figure 2. Male C. bairdi assists molting primiparous female by grasping the old exoskeleton and stroking the emerging carapace.

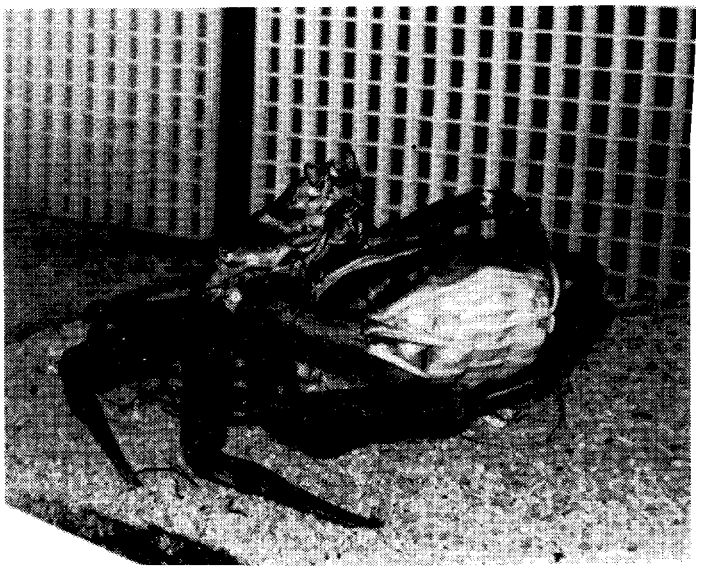

Figure 3. Male C. bairdi assists molting primiparous female by lightly pushing the emerging female outward from the old exoskeleton.

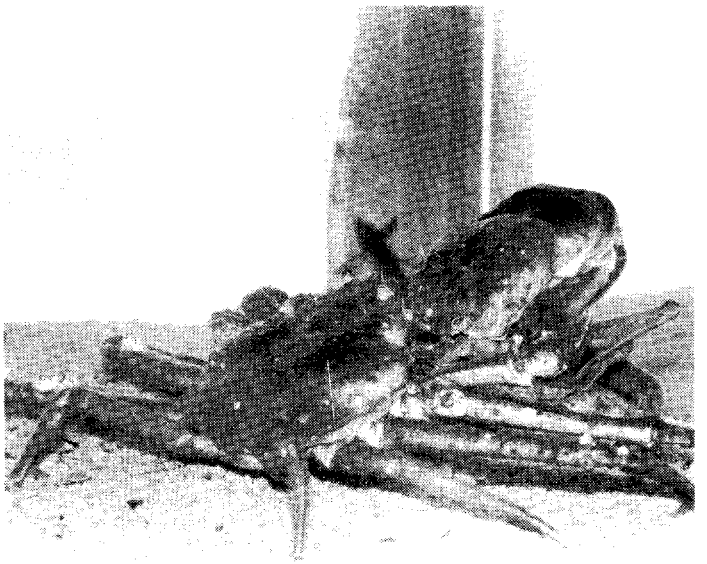

Figure 4. Male C. bairdi assists molting primiparous female by holding onto the anterior portion of her old exoskeleton as she emerges.

PLATE II

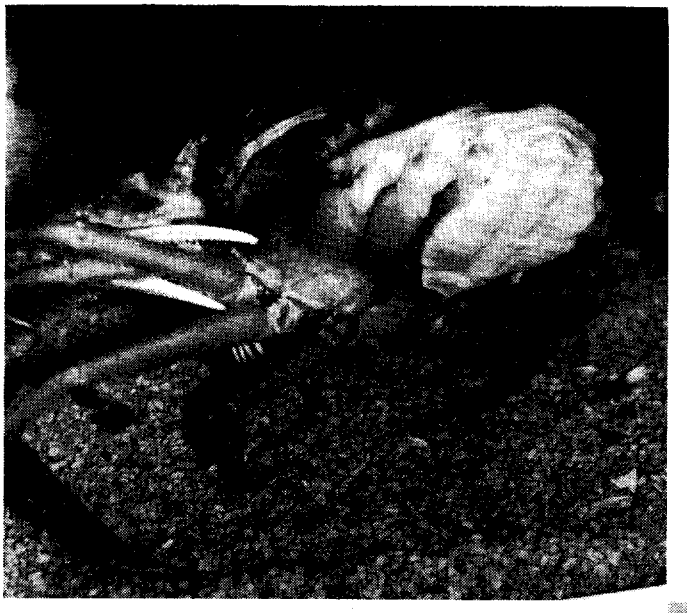

Figure 5. Male C. bairdi assists molting primiparous female by holding her elevated above the substrate while bouncing her.

Figure 6. Male C. bairdi continues to grasp the old exoskeleton of a molting primiparous female as she completes her molt.

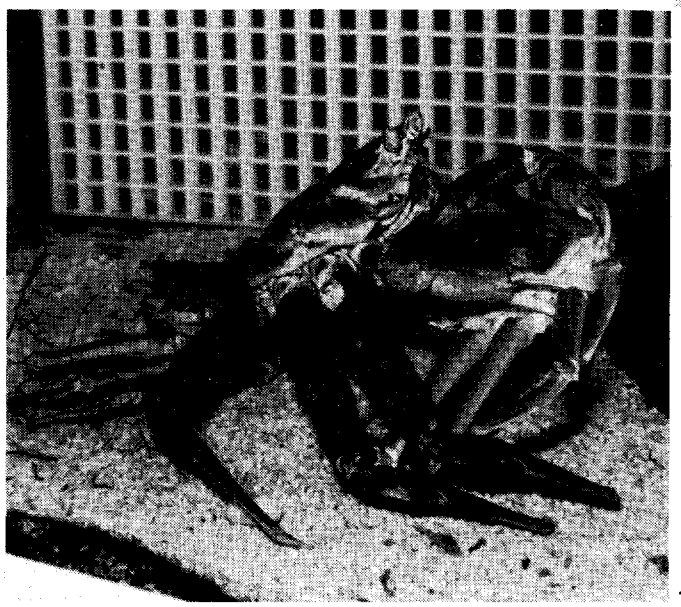

Figure 7. Male C. bairdi grasps softshell primiparous female immediately after she completes her maturity molt.

PLATE III

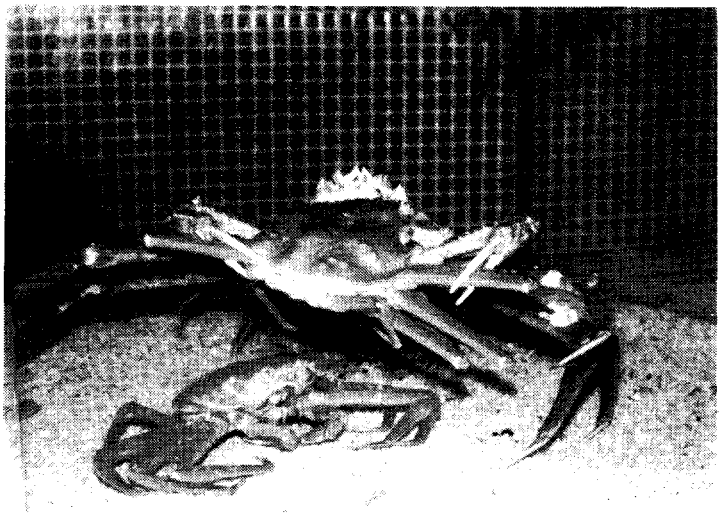

Figure 8. Male C. bairdi continues to grasp softshell primiparous female and begins to position her for copulation. Note the molted carapace in the foreground.

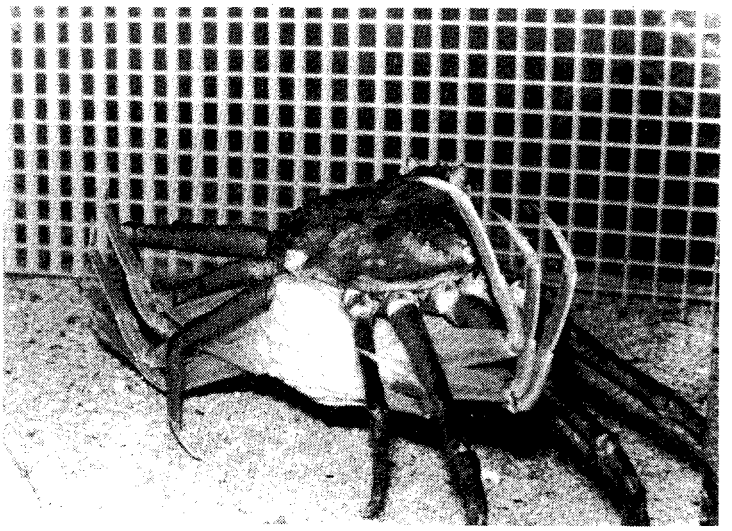

Figure 9. While copulating, this male C. bairdi stands ¾ stance and the female prepares to pull-up.

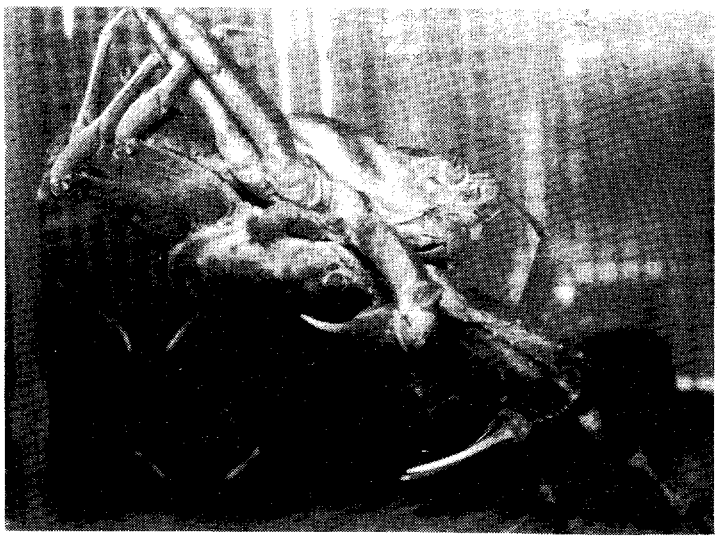

Figure 10. Male (top) and female C. bairdi in the sternum-to-sternum mating position. Male holds the female in position with his right chela.

High-on-Legs (Figure 9)

A crab assumes full stance by rising onto the distal tips of its pereiopods. Males commonly moved high-on-legs: (1) while searching for a molting female or food which was in the immediate vicinity; (2) in agonistic intrasexual interactions over a potential mate; and (3) during the act of intromission (particularly if approached by other males). Females stood high-on-legs: (1) while preparing their pleopods for egg attachment; (2) while grooming developing eggs; and (3) while their eggs hatched. *C. bairdi* of any size or either sex stood high-on-legs while eliminating solid wastes or while experiencing adverse physical/chemical conditions. Under the latter circumstance, the action may continue for hours or until the crab dies or conditions improve. During egg grooming and hatching, a high-on-legs stance is repeated many times (its duration becoming hours); otherwise, the stance is only maintained for minutes.

Antennule Flicking

Antennules are extended and twitched while being rotated to either side or shifted vertically. The only times when *C. bairdi* did not flick their antennules were: (1) during periods of overall quiescence at temperatures below 1°C; and (2) when exposure might lead to their damage. Males which had their antennules removed (in the lab) and those which had lost them naturally were able to locate both mates and food without obvious handicap. Each twitch of the antennules requires only fractions of a second; however, the action is nearly continuous while the crab is alert and moving.

Pushing

After flexing a cheliped inward, a crab touches the broad exterior surface of the propodus against part of another crab's body and exerts outward pressure by extending the chela. Pushing resulted: (1) when a resting crab was disturbed (bumped or stepped on) by an active individual; (2) when one male was grasped by another male (particularly when the graspee was considerably smaller than the grasper; (3) as a form of resistance to mating by female graspees (especially during molting and egg hatching); (4) when a semi-soft-shelled, recently-molted male was grasped or touched by another male; (5) at the time of egg extrusion when a male released the female with which he had copulated; and (6) when a crab with food was touched by one or more competitors. Pushing may continue for many minutes when the grasping relationship is prolonged or, in brief interactions, it may be completed in seconds.

Submissive Posture

Walking legs on each side are positioned close together with their tips pointed inward, chelipeds are held close to the body with fingers touching the mouth parts which are closed, the eyestalks may be depressed within the orbits and the crab is quiescent. The submissive posture is assumed by an individual (be it juvenile or adult, female or male): (1) when grasped by a larger individual; (2) in response to beating actions or body lifting received from a grasping male; or (3) when any crab was stepped upon by another crab several times its size. No crab remained in submissive posture for more than a few minutes at a time.

Stroking (Figure 2)

While holding the graspee with one cheliped, the grasper extends the other cheliped and touches its tips to the surface of the graspee's carapace, abdomen, or pereiopods then moves the tips of the extended cheliped in approximately a straight line over the surface or end of a leg joint. The tips of the cheliped are then lifted and extended to either the same or a new starting point and the motion is repeated. Usually the cheliped was moved in a lateral direction with its tips held at a shallow angle to the contacted surface. Occasionally the motion was directed back-to-front or front-to-back with the cheliped held nearly perpendicular to the surface. Males which exceeded the size of their female partner commonly stroked the extreme posterior edge of the carapace and/or the first abdominal segment. Some smaller males could not reach the female's abdomen while retaining a secure grasp, and consequently tended to stroke the graspee's pereiopods and anterior regions of the carapace. Although each stroke is performed in a few seconds or less, males usually repeat the action for several minutes.

Stroking occurred in most (though not all) matings. Often it was the first action performed by a grasping male subsequent to a graspee's escape attempt. Furthermore, every male that assisted a molting female stroked portions of the female's new exoskeleton as she emerged.

Rubbing

This action is identical to stroking except that portions of the cheliped other than the tips are brought into contact with the graspee's exoskeleton. The inner, lateral, concave face of the cheliped tips (which very closely conforms to the convexly curved exterior surface of the proximal portion of the female's abdomen), the tubercled convex proximal portion of the propodus, and the inferior and superior spines of the propodus are used in rubbing. *C. bairdi* of various sizes and both sexes employed their chelipeds in rubbing and stroking motions while: (1) searching for food in their immediate vicinity; and (2) exploring and contacting large foreign objects. These actions occurred only when the crab was within inches of (or came in contact with) the object of interest.

Poking

After positioning the cheliped(s) at a steep angle to the female's carapace, pereiopods, or abdomen, the male abruptly presses the tips of his cheliped(s) downward in a short, jerking, prodding motion. This action may be repeated many times. While the motion was sufficient to visibly depress a newly molted female's exoskeleton at the point of contact, it did not produce an actual puncture, nor was the impact of poking sufficient to depress the fully sclerotized exoskeleton of a hard-shell female. All soft-shelled and most hard-shelled females temporarily retracted their eyestalks within their orbits immediately after being poked.

Sometimes the grasper poked the graspee with no obvious outward provocation or cue; however, like stroking, it was a common initial response of the grasper when the graspee tried to escape. When both partners were of approximately

equal size, the male generally maneuvered the female into a sternum-to-sternum mating position by poking the posterior edge of her carapace toward his sternum while simultaneously encircling her with his legs.

Body Lifting

Holding the graspee (usually a female) by the pereiopods in one cheliped, the grasper (usually a large male) lifts it high off the substrate and well above the horizontal plane of his own body. In extreme cases, the grasper lifts two or three pairs of his anterior pereiopods off the substrate and turns 360° while holding the graspee aloft. Each body lift lasts less than one minute.

Body lifting typically occurred: (1) when a large grasping male was approached by another large male; (2) as an aspect of a prolonged grasp which commenced prior to the female's molt; or (3) in response to repeated escape attempts by the graspee. Infrequently, a grasping male might body-lift a female during the interim between copulation and release or the graspee might suddenly be lifted for no apparent reason.

In general, the body lift immediately preceded beating. However, body lifts occurring before or during agonistic interactions (between the grasper and a male rival) were separate actions which more or less effectively kept graspees beyond the reach of the rivals. Some small male graspees were also subjected to body lifting.

Bouncing

From a normal rostrum-to-rostrum grasping position, the male holds the graspee by its first pair of periopods and repeatedly raises then lowers the graspee. Some grasping males bounced females prior to their maturity molt, or after the molt but before copulation. However, this action was most common during post-copulatory grasping, when it usually preceded abdominal flapping by the graspee.

Bouncing continued for a period of seconds or minutes. If the female failed to flap her abdomen after being bounced by the male then he might begin body lifting and/or beating her. Performance of this series of events seemed to depend on the size of the grasping male, as very few small males bounced their female partners.

Beating

The grasping male raises one cheliped above the horizontal plane of his carapace then abruptly swings it forward and downward toward the graspee which is held (with the other cheliped) facing rostrum-to-rostrum. A jolting blow was often landed on the graspee's pereiopods or carapace in this manner. Even when a hit was not delivered, the forceful motion alone produced an identical result; that is, the graspee assumed a submissive posture. When the graspee did not become quiescent, beating was usually repeated. The blow was dealt with the graspee held either at the peak of a body lift or within the same horizontal plane as the graspee's body. A single beating motion required little more than one second to complete. Both female and small male graspees were subjected to beating. Confrontations between male rivals also commonly involved beating.

Kicking

One crab quickly strikes directly at the carapace or appendages of another crab with the distal ends of one or both members of the first or second pair of pereiopods. The spiked dactyl was often thus employed, but other joints also served as the striking surface. The kicking motion was generally very rapid and required less than one second from start to finish.

Females (especially multiparous individuals) sometimes kicked grasping males in their efforts to escape from or resist mating with them. Male graspers sometimes kicked female graspees in conjunction with beating. Kicking was also performed: (1) by females when grasped by other organisms; (2) by males involved in competitive interactions over potential mates; and (3) by females in agonistic interactions over food.

Carapace Caressing

Facing the graspee rostrum-to-rostrum, the male presses his two chelipeds against the opposite sides of the graspee's carapace. Contact is between the inner lateral face of each cheliped and the outer lateral surface of the graspee's carapace. Usually the area of contact was small (for example, only the spread cheliped tips were in actual contact). However, small grasping males did, on occasion, press a major portion of the full length of each cheliped against the graspee's carapace. Males usually leg-encircled graspees before releasing their grasps to commence carapace caressing or palpitating. Unrestrained partners demonstrated excellent propensities for escape. Carapace caress duration varied from several seconds to several minutes.

Assisting in Molt (Figures 2-6)

A female which is grasped by a male (of equal or greater size) a few days or hours prior to her maturity molt may receive help from the male as she emerges from the old exoskeleton. With the male positioned rostrum-to-rostrum in front of the female, assistance may be provided in one of the following ways: (1) he may simply stroke and poke soft sections of the female's new carapace as they become exposed (Figure 2) thereby helping to perforate the thick mucous layer located between the new and old exoskeletons; (2) he may lightly push the emerging female outward from the old exoskeleton with one cheliped (Figure 3) or he may hold the anterior portion of her old exoskeleton with one cheliped (Figures 4-6) or he may hold the anterior portion of her old exoskeleton between the proximal sections of both chelipeds and push her with the tips of both; (3) he may body lift the female and gently bounce her during ecdysis; or (4) he may hold the female elevated well above the substrate and perpendicular to it (Figure 5) while bouncing her.

Hungry, hard-shelled females readily attacked and devoured parts of molting females and hungry, hard-shelled males readily attached and devoured parts of molting males. But inter-sexual cannibalism was rare. In one instance, a large male grasped a molting immature female, assisted her to emerge successfully, and then released her immediately afterward. The male showed no further interest in this juvenile female.

Leg Encircling

After positioning itself rostrum-to-rostrum, one crab hooks the dactyls of its anterior-most pereiopods behind the proximal portions of another crabs pereiopods or behind its carapace. The grasper secures its hold by flexing all encircling pereiopods and thereby bringing its carapace into contact with that of the graspee. Once enfolded, the graspee is unable to move freely and is vulnerable to additional manipulations by its captor. Graspers employed this advantage to rub, stroke, or poke the graspee's abdomen, carapace, and/or pereiopods in preparation for, or immediately after, copulation. Although female crabs competing for food tended to leg encircle as long as the morsel lasted, the duration was far less (seconds to a few minutes) in non-mating situations. Males alone resorted to leg encircling while manipulating other crabs as potential mates.

Leg Interposing

While facing the graspee rostrum-to-rostrum, a small grasping male places the distal portions of his pereiopods between the proximal portions of the graspee's pereiopods. Duration of the activity never exceeded ten minutes and sternum-to-sternum positioning usually occurred shortly thereafter. Small males, suspended beneath their female partners during copulation, often interposed legs with them in order to maintain a sternum-to-sternum position. Males and females both interposed their legs with other individuals while attempting to steal food from them.

Extension and Vigorous Movement of Mouth Parts

A crab stretches its maxillipeds outward and rapidly waves flagellae. Movements of the inner oral appendages usually accompany the more obvious outer movements. Extension and vigorous movement of the mouth parts as part of reproductive behavior, were exhibited: (1) by a male immediately before and while he positioned sternum-to-sternum with a female; (2) by a male as he returned the female to an upright position after copulating with her; (3) invariably by both a grasped female and her mate as the female extruded eggs; and (4) by a male when he flapped his abdomen after releasing an extruding female. In reproduction, extension and vigorous movements of mouth parts was usually begun and completed within five minutes.

C. bairdi also performed this action while feeding and defecating. In these contexts, the durations were again quite short (several minutes at most). Small, visible particles suspended in the water around the crabs were drawn toward their oral openings during rapid flagellation. This flow pattern suggests that vigorous movement of these appendages may be important to the collection and close range detection of water soluble substances associated with food or mates.

Abdomen Flapping

A crab lowers its abdomen (such that the distal-most segment is closest to the substrate and all segments are nearly perpendicular to the substrate), holds it open for a few seconds, then flexes it upward to a fully closed position. This action may be repeated many times. Males and females normally flapped their abdomens while defecating. Ovigerous females flapped their abdomens: (1) possibly as a means of brood care to flush foreign and waste material away from the developing eggs and (2) to disperse the larvae as they hatch. Grasping pairs of crabs flapped their abdomens at various times before and after copulating. In some instances, the graspee flapped her abdomen prior to copulation; in fewer cases, the grasping male responded immediately by flapping his abdomen.

The following series of events occurred after most matings: (1) within minutes after dismounting, the male flapped his abdomen while holding the female directly in front (rostrum-to-rostrum); (2) seconds later the female graspee began flapping her abdomen; (3) the female continued flapping at irregular intervals until approximately one-half hour before extruding her eggs; and (4) when the female had extruded most (if not all) of her eggs, the male released his grasp and within seconds began flapping his abdomen.

Some females that mated with smaller males did not flap their abdomens, perhaps because the males did not lift the female high enough off the substrate for sufficient clearance. However, a few females in the grasps of smaller males lifted themselves off the substrate by standing on dactyl tips and flapped.

Palpitating

The male either leg-encircles the female or interposes his legs among hers then rapidly moves the tips of both chelipeds in opening-closing and short, stroking movements across the dorsal surface of the female's carapace. Palpitating did not occur in every mating but was especially common in matings between small males and larger females. It was continued for less than 30 seconds and immediately preceded a male's attempt at sternum-to-sternum positioning, immediately following the act of intromission, or both. Small males tended to palpitate females prior to swinging beneath them into a mating position, whereas large males tended to palpitate immediately after copulating.

Sternum-to-Sternum Positioning (Figures 9 and 10)

Intromission can only be accomplished in *C. bairdi* with the sternal surfaces of the female and male pressed together and with both partners facing in the same direction. This conformation was achieved in several ways. A small male either swung entirely beneath the female (from a rostrum-to-rostrum grasping position) in a single anterior to posterior motion or he tilted himself and the female perpendicular to the substrate while caressing her tightly with his chelipeds held behind her carapace. A large male was usually more direct. First he rose to about two-thirds or three-quarters of his full stance and spread his pereiopods widely apart. Then, grasping the female with one cheliped, he simply turned her upside down (but facing in the same direction) and placed her beneath himself sternum-to-sternum. Finally, the male pressed his free cheliped beneath the female's carapace thus assuring close contact (Figure 10). In some instances

a large male folded the female's pereiopods thereby positioning her carapace on the substrate, leg-encircled the female, and placed one or both chelipeds behind the female's abdomen. He then used his cheliped(s) and longer pereiopods to pull the female toward himself while pushing upward (lifting) with his shorter pereiopods. As a result, the coupled animals became situated perpendicular to the substrate and sternum-to-sternum.

By no means was sternum-to-sternum positioning always smoothly and easily accomplished. Small males, particularly, erred by positioning off-center. Even large males occasionally erred by pushing the female too far posteriorly.

Intromission (Figure 9)

Direct physical transfer of spermatophores and seminal fluids from the male's reproductive tract to the female's spermathecae constitutes intromission. Before intromission can occur the female must cooperate by lowering her abdomen during the sternum-to-sternum positioning (Figure 9), and the male's first pleopods must be inserted into the female's gonopores. Males accomplish the latter act by lowering and spreading their pleopods while precisely adjusting their position relative to the female.

Copulation was of longer duration (mean value of 24.5 minutes for 15 cases) when multiparous females mated than when primiparous females mated (mean value of 13.7 minutes for 101 cases) (Adams 1982). Among the primparous matings, intromission duration tended to directly increase with amount of elapsed time between molting and mating.

After completing intromission, males which equalled or exceeded the size of their female partners quickly assumed a postcopulatory embrace rostrum-to-rostrum grasping position. Small males usually required more time (up to 30 minutes) to begin postcopulatory embrace.

Pull-up (Figures 9 and 10)

Abrupt, simultaneous contractions of all pereiopods on both sides or alternating contractions on opposite sides of the female's body are used to pull her closer to the male during intromission. The second method mentioned manifested as an apparent swivelling motion of the female beneath the male. Females performed pull-up only when their male partners stood sufficiently elevated above the substrate to permit clearance between the upside-down female and the substrate. Such potential was realized by males whose size (carapace width) equalled or exceeded that of their female partners. Multiparous females tended to pull-up to a greater extent than did primiparous females. Each pull-up was completed in less than five seconds and the action was usually repeated a number of times.

Maxilliped Tap

A grasping male gently and briefly presses the tips of one cheliped against the female's maxillipeds while the couple is copulating. Usually the male performs this action immediately after the female does a pull-up from beneath. The female becomes quiescent during the maxilliped tap and often remains so for a minute or longer afterward. When the female performs a number of pull-ups,

the male may leave one cheliped positioned just above her maxilliped and tap several times or even leave the cheliped tips pressed against them in continuous contact for several minutes.

Pleopod Combing

A female elevates her body to at least three-quarters stance, completely lowers her abdomen, reaches the tips of one cheliped among her pleopods, and closes the tips around the proximal portion of a pleopod. She then moves the cheliped forward thereby drawing the pleopod between its lightly appressed tips. Frequently the female continues moving the cheliped forward and the tips pass over the opened mouth parts.

Pleopod combing was performed by all multiparous females during the late stages of larval hatching and prior to extrusion of the new egg mass. The behavior was repeated until all or nearly all empty egg cases had been removed. Although each combing action lasted less than one minute, the effort of completely cleaning the pleopods totaled many hours and spanned several days. During the long egg-bearing period, both primiparous and multiparous females gently combed portions of their pleopods perhaps culling out inviable eggs and debris.

Clasping and Pulling at Pleopods

(1) By females. An individual partially or fully lowers her abdomen then reaches the tips of one cheliped among the pleopods, closes the tips on a single pleopod, and lightly tugs outward. This action occurred uniquely as part of the preparations which females made prior to extrusion of their eggs. It lasted only seconds but was commonly repeated several times. Primiparous females also positioned the pleopods by moving them (with cheliped tips) to conform to the abdomen's perimeter and some even pressed the cheliped tips against the innter concave surface of their abdomens (which had not yet sclerotized into a rigid shape).

(2) By males. After flapping its abdomen and extending the distal tips of its first pair of pleopods downward (away from the sternum), a male reaches the tips of one cheliped toward the first pleopods and closes the tips upon them. The male then lightly tugs anteriorly on the pleopods. Few individuals actually pulled on their pleopods, although many males reached a cheliped very close to the exposed appendages. This action was performed minutes after the male released a female with which he had copulated. It was very brief, lasting only seconds, and was not repeated more than once per mating.

Pleopod Waving and Flexing

(1) By females. Soon after copulating, a grasping male *C. bairdi* usually flaps his abdomen until the female graspee also begins flapping. Although the male ceases flapping within a few minutes, the female slowly increases the duration of her own flapping over the next half hour then starts to prepare her pleopods for impending egg attachment. These preparations include: (1) waving and flexing; (2) clasping and pulling; and (3) combing. Initially, the female lifts each pair of pleopods independently so that it is separated from its nearest neighbor(s) by a small space. In a short time she is able

to fan or wave them vertically as individual pairs throughout the space between her sternum and fully lowered abdomen. The exercise becomes more complex as she simultaneously begins contracting and expanding (flexing) each pair latero-medially. As each pair is lifted toward her sternum they are simultaneously stretched laterally outward. Then, as the pleopod pair is lowered, each member is curled medially inward. At the completion of such preparations, a female's pleopods resemble a hemisphere formed by concentric layers of feathery brushes which expand and contract synchronously, *C. bairdi* females wave and flex their pleopods: (1) in preparation for egg extrusions; (2) during the prolonged egg-bearing period; and (3) periodically throughout the larval hatching period.

(2) By males. As a prelude, the crab rises to two-thirds or a greater fraction of his full stances and lowers his abdomen until it is nearly perpendicular to his sternum. He then swings the distal ends of the first pleopods downward, sometimes moving them latero-medially as well. The first pleopod pair may be held extended downward for a few seconds before being raised toward the sternum. This action may be repeated several times with or without abdominal flapping between each repetition. Males continued this action irregularly for approximately 15 minutes and terminated it by returning the abdomen to a fully raised position. Male pleopod waving and flexing was observed: (1) minutes after the end of intromission (during postcopulatory grasping); and (2) seconds after the male released the female (following extrusion of her eggs).

Stretching

All walking legs and the cheliped on one side of the body are extended and spread laterally outward to their maximum extent. The tips of the cheliped may even be stabbed into the substrate during this action. Mouth parts on the same side are also extended as far as possible. Simultaneously, the limbs on the opposite side of the body remain in a normal flexed position so that the stretched side is closer to the substrate. This action was continued for as long as one minute but was not repeated within a single observation period (12 hours).

This infrequent behavior was performed by males shortly after termination of the postcopulatory embrace. It was also performed in isolated instances outside of the reproductive season by juveniles, adult females, and adult males under non-mating circumstances.

General Format of Mating Behavior

Elements of decapod mating behavior are usually described in reference to the three major periods before, during, or after key event-copulation. Hence the adjectives precopulatory, copulatory, and postcopulatory have become common temporal descriptors. All actions described in this paper have been identified with respect to these periods in Table 2. In completed matings, each of these three successive periods is demarcated by the performance of specific actions. The precopulatory period commences with initial grasping of the female by the male and ends with sternum-to-sternum positioning of the male and female and simultaneous relaxation of their abdomens. The copulatory

Table 2. Duration of Tanner crab, *Chionoecetes bairdi*, mating behavior actions.

Mating Behavior Action [1]	Primiparous females		Multiparous females
	Grasped before molt	Grasped after molt	
High-on-legs	Sec. to hrs.	Sec. to min.	Sec. to hrs.
Grasping	Min. to days	Min. to hrs.	Hrs. to days
Antennule flicking	Min. to days	Min. to hrs.	Hrs. to days
Pushing	Sec. to min.	Sec.	Sec. to min.
Submissive posture	Min.	Min.	Min.
Stroking	Min. to hrs.	Min.	Min. to hrs.
Rubbing	Min. to hrs.	Min.	Min. to hrs.
Poking	Min.	Sec. to min.	Min.
Body lifting	Sec. to min.	Sec.	Sec. to min.
Bouncing	Min.	Min.	Min.
Beating	Sec. to min.	Sec.	Sec. to min.
Kicking	Sec.	Sec.	Sec. to min.
Carapace caressing	Sec.	Sec.	Not observed
Assisting in molt	Min.		
Leg encircling	Min.	Min.	Min.
Leg interposing	Sec.	Sec.	Not observed
Vigorous movement of mouth parts	Min.	Min.	Min.
Abdomen flapping	Sec. to min.	Sec. to min.	Sec. to min.
Palpitating	Sec.	Sec.	Sec.

-Continued-

Table 2. Duration of Tanner crab, *Chionoecetes bairdi*, mating behavior actions (continued).

Mating Behavior Action[1]	Primiparous females		Multiparous females
	Grasped before molt	Grasped after molt	
Sternum-to-sternum positioning	Min.	Min.	Min.
Intromission	Min.	Min.	Min.
Pull-up	Sec.	Sec.	Sec.
Maxilliped tap	Sec.	Sec.	Sec.
Pleopod combing	Sec. to min.	Sec. to min.	Hrs.
Clasping and pulling at pleopods	Sec. to min.	Sec. to min.	Sec. to min.
Pleopod waving and flexing	Min. (female) Sec. (male)	Min. (female) Sec. (male)	Min. (female)[2] Sec. (male)
Stretching	Sec.	Sec.	Sec.

[1] Abbreviations for normal durations of action are: sec., ≧ one second but less 60 seconds; min. ≧ one minute but less than 60 minutes; hrs. ≧ one hour but less than 24 hours; and days, ≧ 24 hours.

[2] As a part of copulation, this action only continued for seconds. However, when multiparous females dispersed their hatching larvae it lasted for minutes or hours.

period begins as the male inserts his first pair of pleopods into the female's gonopores and ends as he withdraws them. The postcopulatory period starts as the male moves out of the sternum-to-sternum position to resume a rostrum-to-rostrum grasping position and ends as he releases the female (nearly always at the time she extrudes the new egg mass).

Characteristic and Essential Elements of Mating Behavior

Of all the actions noted above, only five (grasping, sternum-to-sternum positioning, abdomen flapping, vigorous movements of mouth parts, and intromission) were observed in every completed mating. As indicated in Table 1, palpitating, carapace caressing, body lifting, bouncing, and sternum-to-sternum positioning were performed only by males and exclusively as elements of mating behavior. Females, alone, were observed to pull-up during copulation.

Breeding transpired only when: (1) a male responded to a female's presence and initiated mating behavior by grasping her; (2) the male was sufficiently large to withstand resistance and agonistic actions from the female; (3) the male continued to grasp until mating was physically possible; (4) the male succeeded in properly positioning sternum-to-sternum with the female; (5) the female cooperated by lowering her abdomen during sternum-to-sternum positioning; and (6) the male lowered his abdomen to expose his first pair of pleopods. The performance sequence of mating behavior action is presented in Table 3.

Factors Affecting Action Duration and Performance

The duration of each action varied from one mating to another (Table 3). Factors affecting the duration of specific actions included: (1) previous mating experience of the female - whether primiparous of multiparous (Adams 1982); (2) primiparous female carapace condition at the onset of grasping - whether approaching the maturity molt or recently molted; (3) relative sizes of the male and female; and (4) the number of males available as mates and the extent of competitive interaction between them.

Extensive precopulatory relationships (varying from one to twelve days) commonly developed when large males grasped either primiparous females several days prior to their molt to maturity or multiparous females whose eggs were in the process of hatching. Stroking, rubbing, poking, body lifting, beating, bouncing, and kicking were repeated again and again in both cases. Multiparous females usually removed empty egg cases from their pleopods as larvae hatched and usually resisted mating attempts by grasping males during this time. Prolonged pleopod waving, flexing, and combing actions were performed by ovigerous, multiparous females.

Agonistic interactions were common among males when more than one male was present with a mateable female. Interactions between a male and a female were usually mild (involving little more than grasping and pushing) when the female was primiparous. Even so, 42 males engaged in 21 fights over primiparous females. The victors in 18 fights were the larger individuals. Of the three crabs which were victorious over larger opponents, one had a harder exoskeleton than his opponent, another chased his opponent away from a female that had molted to maturity 25 days previously, and in the final case the larger male, unexplainably discontinued its grasp.

Table 3. Performance sequence of Tanner crab, *Chionoecetes bairdi*, mating behavior actions (x = behavior performed).

Sequence	Precopulatory period	Copulatory period	Postcopulatory period
Actions:			
High-on-legs	X	X	X
Grasping	X	X	X
Antennule flicking	X	X	X
Pushing	X		X
Submissive posture	X		X
Stroking	X		X
Rubbing	X		X
Poking	X	X	
Body lifting	X		X
Bouncing	X		X
Beating	X		X
Kicking	X		X
Carapace caressing	X		X
Assisting in molt	X		
Leg encircling	X		X
Leg interposing	X	X	
Vigorous movement of mouth parts	X	X	X
Abdomen flapping	X		X
Palpitating	X		X
Sternum-to-sternum positioning	X		
Intromission		X	
Pull-up		X	
Maxilliped tap		X	
Pleopod combing	X		X
Clasping and pulling at pleopods			X
Pleopod waving and flexing			X
Stretching			X

It was not uncommon for several small males to simultaneously grasp the same female with the eventual outcome that the female escaped from their combined holds. Such interference between small males involved mutual grasping, pushing, leg interposing, and stroking.

Interactions were more forceful when multiparous females were grasped and defended. Only large males (exceeding 120 mm carapace width) successfully competed for and copulated with multiparous females. Their agonistic interactions involved exchanges of violent blows to the carapace and legs (with chelipeds) and severe grasps to legs and body. As a result, most of these males suffered breaks or splits in the tips or spines of the claws and/or exoskeleton of the legs or carapace.

Two factors, exoskeletal flaccidity and limb loss, definitely prevented some males from mating. Recently molted males as well as intermolt males were responsive toward primiparous females which were molting or had recently molted. Two partially soft (postmolt) males, with carapace widths of 113 mm and 128 mm, grasped soft, newly molted primiparous females which escaped (without copulating) within six hours. However, exoskeletal flaccidity only temporarily restricts male mating potential. Twenty-six days after it molted, another partially soft male, measuring 113 mm carapace width, successfully copulated with a soft-shell, primiparous female. Three males which were in early stages of ecdysis also successfully copulated with females. One of the males (measuring 115 mm carapace width) mated four days prior to molting; the other two (measuring 115 mm and 120 mm carapace width) mated only two days before molting.

Possession of at least one cheliped was an essential prerequisite for proper sternum-to-sternum positioning and copulation. This was clearly demonstrated when three males, which had each lost both chelipeds, were separately placed in aquaria with very soft primiparous females. Each hard, new-shelled male responded to a nearby female by either standing at an elevated stance and actively moving his mouth parts or by moving toward the female and subsequently encircling her with his pereiopods. Two of the males used their pleiopods in attempts to pull the female into a sternum-to-sternum position but both males lacked sufficient leverage to complete this maneuver.

Polyandry

Under certain circumstances, females mated with more than one male. Six very soft, newly molted, primiparous females were released by small grasping males after copulating and before extrusion of the egg masses. During that interim, each female was grasped by and copulated with another male.

One multiparous female mated with a large male before her entire brood of larvae hatched. Additional matings occurred during the lengthy period in which she cleaned her pleopods of empty egg cases (preparatory to the impending extrusion of the new egg clutch).

DISCUSSION

Numerous studies of brachyuran mating behavior have been reported in the literature. Therefore, similarities and differences between *Chionoecetes bairdi* and other species can be readily identified. The animal's morphology, reproductive cycle, and the extent to which males display courtship and agonistic behavior are particularly useful subjects for such comparisons.

Inherent similarities of body structures and their organization place some limitations on the range of movements a related group of organisms can perform and positions they can assume. For example, the ventral location of the gonopores and the horizontal rigidity of the cephalothorax in all male and female brachyurans make sternum-to-sternum positioning an absolute prerequisite to intromission. In fact, nearly all behavioral elements observed for *C. bairdi* have been reported for other brachyuran crabs. A few examples of such identical behavioral elements are noted in Table 4.

In the first published general review of brachyuran mating behavior, Hartnoll (1969) recognized two patterns: (1) The male carries a premolt female throughout a prolonged courtship. He may assist her during her maturity molt or release her momentarily until she emerges on her own. Copulation occurs very soon after the molt and a postcopulatory embrace is resumed until the female's exoskeleton hardens or (2) a brief courtship (varying from virtually indistinguishable to very complex) precedes copulation between a hard-shelled male and hard-shelled female. There is no postcopulatory attendance by the male. In an uncommon variation of this pattern, the hard-shelled female is carried by the male for several days before mating. Hartnoll (1969) remarked that at least two species in the family Majidae diverge from these basic schemes. *Hyas coarctatus* males were observed mating with freshly molted females but apparently did not display any interest prior to the molt. *H. coarctatus* and *Maia squinado* (and probably *Pugettia producta*) females, when given the opportunity, mate when the female is soft in some instances and hard-shelled in others (Hartnoll 1969).

Laboratory observations of *C. bairdi* mating behavior suggest that this majid crab further deviates from the two general reproductive patterns (purported by Hartnoll 1969) in the following ways: (1) After the maturity molt, primiparous females were not reproductively constrained by carapace condition. They were able to mate in a soft-shell condition (immediately or soon after molting) or in a semi-hard-shell condition (as late as three weeks after molting). (2) Small males and some very large males mated with soft females after only a brief period of attendance. At the time of release, the ovigerous females still have soft exoskeletons. (3) Multiparous females, which are all hard-shelled, were generally carried by males for a long period (as much as several days) before copulating.

Agnostic behavior is developed to varying extents from mildly jostling to severely injurious in different brachyuran crabs. Strong aggression was only displayed by *C. bairdi* during feeding and mating. Within limits, the hungrier the crabs the more aggressively they competed for food. Males generally handled molting, primiparous females gently (particularly after they emerged).

Table 4. Reported brachyuran mating behavior actions identical to those of Tanner crab, *Chionoecetes baird*[1].

Taxonomic identification	Author(s) and Year(s) of publication	Behavioral actions[2]
Family Cancridae		
Cancer magister	Snow & Neilsen 1966	High-on-legs
		Grasping
		Stroking
		Body lifting
		Leg encircling
		Vigorous movement of mouth parts
		Sternum-to-sternum positioning
Family Grapsidae		
Pachygrapsus crassipes	Hiatt 1948	Grasping
		Pushing
		Leg interposing
		Sternum-to-sternum positioning
		Abdomen flapping
		Pleopod combing
		Clasping and pulling at pleopods
		Pleopod waving
Sesarma cinereum	Seiple & Salmon 1982	Pushing ("claw push")
		Leg encircling
		Kicking ("leg kick")
		Palpitating ("carapace touch")
		Sternum-to-sternum positioning ("pair")
Family Portunidae		
Callinectes sapidus	Teytaud 1971	Grasping
		Submissive posture
		Beating
		Sternum-to-sternum positioning

[1] Although some of these actions are not specifically named, their descriptions in the cited literature match the definitions given in this paper.

[2] Terms enclosed in parentheses and quotation marks are those of the authors cited.

No detectable marks were observed on female *C. bairdi* as a result of precopulatory or postcopulatory embraces. Gentle behavior toward the female has also been noted in *Cancer magister* (Snow and Nielson 1966), *Cancer pagurus* (Edwards 1966), and *Menippe mercenaria* (Binford 1913). Although *C. bairdi* males occasionally participated in wild fights over primiparous females, none of the fights led to loss of limb or life. Injury-free combat has also been reported for the majid crab *Maia squinado* (Carlisle 1957).

Matings involving multiparous *C. bairdi* females were noticably more aggressive and competitive. Fights were common between competing males and often led to broken or severed limbs. In contrast with primiparous females, all mated multiparous females bore fresh, deep grasping abrasions on the meri of their pereiopods.

Different mating behavior patterns may contain many identical actions, yet considerable differences may still exist in the sequence of actions, in their duration and in the total assortment of actions which are performed. Several of the mating behavior actions reported for two other majid crabs, *Chionoecetes opilio*, and *Libinia emarginata*, are identical to those of *C. bairdi* (Table 5). Nevertheless, each pattern of mating behavior also has unique attributes. For instance, only male *L. emarginata* perform obstetrical behavior[1] (Hinsch 1968). The primary behavioral differences between the congeners *C. bairdi* and *C. opilio* pertain to the duration of some actions. In matings of primiparous *C. bairdi*, the duration of intromission averaged eight minutes when it occurred less than six days after the female's maturity molt (Adams 1982). This is significantly less than the average 43 minutes intromission duration reported for primiparous *C. opilio* which mated less than five days after molting (Takeshita and Matsuura 1980).

Two discrepancies exist in the published descriptions of *Chionoecetes* spp. mating behavior. Takeshita and Matsuura (1980) report that a grasping male places the female upon her back on the substrate and holds her in that position as he initiates intromission. Watson (1970 and 1972) has not reported this means of positioning in *C. opilio*; nor was such behavior noted in this study of *C. bairdi*. Watson also described the release of spermatophores by *C. opilio* males during all seven postcopulatory embraces which he observed. However, Takeshita and Matsuura (1980) did not observe this phenomenon for either *C. opilio* or *C. bairdi*. *C. bairdi* males in the present study emitted spermatophores during the postcopulatory period in only two out of 133 matings.

In all other respects, the results of this study corroborate the earlier results of Watson (1970 and 1972) and Takeshita and Matsuura (1980). These earlier works made excellent use of a limited number of meetings; however, their small sample sizes were insufficient for a complete description of mating behavior.

---

[1] Obstetrical behavior includes active searching, aggressive behavior, and protecting the female by grasping in a sternum-to-sternum position while she releases her larvae and cleans her pleopods.

Table 5. Reported mating behavior actions of *Chionoecetes bairdi* identical to those reported for two other Majid crabs.

Taxonomic identification	Author(s) & year(s of publication	Behavioral actions
Family Majidae	Watson 1970 & 1972	High-on-legs
Chionoecetes opilio		Grasping
		Pushing
		Stroking
		Assistance in molt
		Vigorous movements of mouth parts
		Sternum-to-sternum positioning
		Abdomen flapping
		Pleopod waving
Chionoecetes opilio	Takeshita and Matsuura 1980	Grasping
		Body lifting
		Sternum-to-sternum positioning
		Abdomen flapping
		Pleopod combing
		Clasping and pulling at pleopods
		Pleopod waving
Libinia emarginata	Hinsch 1968	High-on-legs
		Grasping
		Submissive posture
		Sternum-to-sternum positioning
		Abdomen flapping
		Pleopod combing

Earlier in this paper we noted that there were extensive precopulatory relationships (1-12 days) for *C. bairdi*. However, we observed no movements by the male which might entice or attract receptive partners. Production of a pheromone has been implicated in reproductive behavior in many arthropods. Ryan (1966) established the presence of a pheromone in the portunids. This may be the key to *C. bairdi* recognition but the hypothesis remains to be tested. Perhaps in the absence of obvious display actions, high-on-legs movements and body lifting and beating emphasize the size and strength of the male. Body lifting and beating consistently produced temporary quiescence in active female graspees. However, these actions were not always performed and some interactions advanced directly from grasping to intromission. Therefore, the courtship phase of *C. bairdi* crab's reproductive behavior seems to consist primarily of male attendance (through grasping) to the female with inclusion of additional actions (body lifting, beating, and kicking) when the female persists in trying to escape or in resisting mating. The female's escape attempt and resistance during courtship are equally important to reproductive success because only those males which could withstand these tests of strength and agility contributed to the production of viable offspring.

ACKNOWLEDGMENTS

We thank the following Alaska Department of Fish and Game personnel: William Colgate and David Hicks, for their efforts in shipboard collection and transportation of crabs, and Gordon Kruse for editorial advice, Sharon Theis for her dedication in typing this manuscript, and the Seward Marine Science Center (operated by the Institute of Marine Science, University of Alaska, Fairbanks) which provided the housing and laboratory facilities and some equipment which were essential to this study.

LITERATURE CITED

Adams, A.E. 1982. The mating behavior of *Chionoecetes bairdi*. In: Proc. Int. Symp. Genus *Chionoecetes*, pp. 233-271. Fairbanks, Alaska: Alaska Sea Grant Program, University of Alaska.

Adams, A.E. and A.J. Paul. 1983. Male parent size, sperm storage and egg production in the crab *Chionoecetes bairdi* (Decapoda, Majidae). Int. J. Invert. Reprod. 6, 181-187.

Binford, R. 1913. The germ-cells and the process of fertilization in the crab, *Menippe mercenaria*. J. Morph. 24: 147-204.

Bright, D.B. 1967. Life histories of the king crab, *Paralithodes camtschatica*, and the "Tanner crab", *Chionoecetes bairdi*, in Cook Inlet, Alaska. Ph.D. thesis, University of Southern California.

Brown, R.B. and G.C. Powell. 1972. Size at maturity in the male Alaskan Tanner crab, *Chionoecetes bairdi*, as determined by chela allometry, reproductive tract weights, and size of precopulatory males. J. Fish. Res. Bd. Can. 29: 423-427.

Brunel, P. 1962. Troisieme serie d'observations sur la biologie et la biometrie due crabe-araignee *Chionoecetes opilio* (Fabr.). Rapp. Stn. Biol. mar. Grande-Riviere 1962, 81-89.

Carlisle, D.B. 1957. On the hormonal inhibition of moulting in decapod Crustacea, 2. The terminal anecdysis in crabs. J. Mar. Biol. Ass. U.K. 36, 291-307.

Colgate, W.A. 1982. A review of the Gulf of Alaska Tanner crab, *Chionoecetes bairdi*, fishery and management related research. In: Proc. Int. Symp. Genus *Chionoecetes*, pp. 41-69. Fairbanks, Alaska Sea Grant Program, University of Alaska.

Donaldson, W.E., R.T. Cooney, and J.R. Hilsinger. 1981. Growth, age, and size at maturity of Tanner crab, *Chionoecetes bairdi*: M.J. Rathbun, in the northern Gulf of Alaska (Decapoda, Brachyura). Crustaceana 40(3): 286-302.

Edwards, F. 1966. Mating behavior in the European edible crab *(Cancer pagurus* L.). Crustaceana 10: 23-30.

Garth, J.S. 1958. Brachyura of the Pacific Coast of America. Oxyrhyncha. Allan Hancock Pacific Expeditions. 21 (Pt. I). Los Angeles: University of Southern California Press.

Hartnoll, R.G. 1969. Mating in the Brachyura. Crustaceana. 16:161-181.

Haynes, E., J.F. Karinen, J. Watson, and D.J. Hopson. 1976. Relation of number of eggs and egg length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering Sea and *C. opilio* from the Gulf of St. Lawrence. J. Fish. Res. Bd. Can. 33: 2592-2595.

Hiatt, R.W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pac. Sci. 2: 135-213.

Hilsinger, J.R. 1975. Aspects of the reproductive biology of female snow crabs, *Chionoecetes bairdi*, Rathbun, from Prince William Sound, Alaska. M.S. thesis, University of Alaska, Fairbanks.

Hilsinger, J.R. 1976. Aspects of the reproductive biology of female snow crabs, *Chionoecetes bairdi* Rathbun, from Prince William Sound and the adjacent Gulf of Alaska. Mar. Sci. Commun. 2: 201-225.

Hilsinger, J.R., W.E. Donaldson, and R.T. Cooney. 1975. The Alaska snow crab *Chionoecetes bairdi*: size and growth. Alaska Sea Grant Rep. 75-12, 38 pp. Fairbanks: University of Alaska.

Hinsch, G.W. 1968. Reproductive behaviour in the spider crab, *Libinia emarginata* (L.). Biol. Bull. Mar. Biol. Lab., Woods Hole, 135: 273-278.

Hosie, M.J. 1974. Southern range extension of the Bairdi crab, *Chionoecetes bairdi* Rathbun. Bull. Japan Sea Reg. Fish. Res. Lab. 11: 65-76.

Ito, K. 1963. A few studies on the ripeness of eggs of zuwai-gani, *Chionoecetes opilio*. Bull. Japan Sea Reg. Fish. Res. Lab. 11: 65-76.

Ito, K. 1970. Ecological studies on the edible crab, *Chionoecetes opilio* (O. Fabricius) in the Japan Sea. III. Age and growth as estimated on the basis of the seasonal changes in the carapace width frequencies and the carapace hardness. Bull. Japan Sea Reg. Fish. Res. Lab. 22: 81-116.

Kanno, Y. 1972. Relative growth of the Tanner crab *(Chionoecetes opilio)* in the Okhotsk Sea and differences in two fishing grounds. Scient. Rep. Hokkaido Fish. Exp. Stn. 41:403-411.

Kon, T. 1974. Fisheries biology of the Tanner crab. VI. On the number of ovarian eggs and eggs held in the pleopods. Bull. Jap. Soc. Scient. Fish, 40: 465-469.

Kon, T. 1980. Studies on the life history of the zuwai crab, *Chionoecetes opilio* (O. Fabricius). Spec. Publs. Sado Mar. Biol. Stn. 2, 64 pp. Niigata, Japan: Niigata University.

Kon, T., M. Niwa, and F. Yamakawa. 1968. Fisheries biology of the Tanner crab. II. On the frequency of molting. Bull. Jap. Soc. Scient. Fish. 34: 138-142.

Paul, A.J. 1982. Mating frequency and sperm storage as factors affecting egg production in multiparous *Chionoecetes bairdi*. In: Proc. Int. Symp. Genus *Chionoecetes*, pp. 273-281. Fairbanks, Alaska: Alaska Sea Grant Program, University of Alaska.

Ryan, E.P. 1966. Pheremone evidence in a decapod crustacean. Science, 152: 340-341.

Seiple, W. and M. Salmon. 1982. Comparative social behavior of 2 graspid crabs, *Sesarma reticulatum* and *Sesarma cinereum*. J. Exp. Mar. Biol. Ecol. 62: 1-24.

Sinoda, M. 1968. Studies on fishery of zuwai crabs in the Japan Sea. I. The growth. Bull. Jap. Soc. Scient. Fish. 34: 185-190.

Snow, C.D. and J.R. Nelson. 1966. Premating and mating behavior of the Dungeness crab *(Cancer magister* Dana). J. Fish. Res. Bd. Can. 23: 1320-1323.

Somerton, D.A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 37: 1488-1494.

Somerton, D.A. 1981. Regional variation in the size of maturity of two species of Tanner crab *(Chionoecetes bairdi* and *C. opilio)* in the eastern Bering Sea, and its use in defining management subareas. Can. J. Fish. Aquat. Sci. 38: 163-174.

Takeshita, K. and S. Matsuura. 1980. Mating and egg laying in Tanner crabs. Bull. Far Seas Fish. Res. Lab.

Teytaud, A.R. 1971. The laboratory studies of sex recognition in the blue crab *Callinectes sapidus*. Sea Grant Tech. Bull. 15, 63 p. Miami, Florida: University of Miami.

Thompson, R.J. 1979. Fecundity and reproductive effort in the blue mussel *(Mytilus edulis)*, the sea urchin *(Strongylocentrotus droebachiensis)*, and the snow crab *(Chionoecetes opilio)* from populations in Nova Scotia and Newfoundland. Fish. Res. Bd. Can. 36: 955-964.

Watson, J. 1969. Biological investigations on the spider crab, *Chionoecetes opilio*. Can. Fish. Rep. 13: 24-47.

Watson, J. 1970. Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Bd. Can. 27: 1607-1616.

Watson, J. 1972. Mating behavior in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Bd. Can. 29: 447-449.